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NOTES ON CULTIVATED PLANTS

BY

B. K. BOOM

(*Wageningen*)

(*received February 3th, 1955*)

Setcreasea purpurea sp. nov. (*Commelinaceae*).

S. brevifoliae (Torr.) Schum. & Sydov affinis, caulibus, foliis bracteisque pulchre purpureoviolaceis, calyce glabra, corolla rosea, filamentis subglabris differt.

Planta perennis, ad 40 cm alta. Caulis suberectus vel ascendens, purpureoviolaceus, lineis viridibus notatus. Folia sessilia, oblonga, acuta, basi amplexicaulia, margine longe ciliata, supra glabra vel pilis ± arachnoideis albis obsita, obscure purpureoviolacea, pruinosa, basi virentia, subtus glabra, purpurea, basalia rosulata, 14–18 cm longa, 2–2,7 cm lata, caulinia minora. Vagina 1–2,5 cm longa, ciliata. Inflorescentia pauciflora, sessilis, bracteis involucrantibus 2, acuminatis, sessilibus, bracteolis triangularibus, membranaceis. Pedicelli ± 4 mm longi, glabri, apice longe albopilosi. Sepala 8–10 mm longa, oblonga, glabra. Petala 15–20 mm longa, pallide purpurea, basi cuneata, ± connata. Filamenta ± aequilonga, basi corollae adnata, purpurea, exteriora glabra vel pilis 1–2, interiora pilis 3–8 obsita, antheris aureis. Ovarium glabrum. Capsula?
Habitat: Mexico.

I found this fine plant in the botanical gardens at Darmstadt (Germany) without a name. The curator of this garden, Mr. F. Boerner, informed me that Mr. C. A. Purpus, who travelled in the beginning of this century in Central and North America, introduced this species together with a lot of Orchids. He sent many plants to his brother, the curator of the botanical gardens at Darmstadt.

The genus *Setcreasea* is indigenous to Mexico and adjacent countries. *S. purpurea* comes near to *S. brevifolia* (Torr.) Schum. & Sydov, the latter being distinguished by shorter and green leaves, the white corolla and pilose stamens. From *S. buckleyi* Johnst. (*Tradescantia speciosa* Buckley non L.) our plant differs in the more robust habit, the purple colour of the vegetative parts and the nearly glabrous filaments.

The colour of the leaves varies and depends with cultivated plants on the conditions in the glasshouse. Well cultivated the colour underneath the leaves comes the nearest to H. C. C. 934/3 (Plum-purple), the colour of the top is not determinable with this chart. The colour of the petals is H. C. C. 634/1 (Cobalt-violet).

The type is in the Rijksherbarium, Leiden, coll. *Boom mo. 28046.* This plant seems to be most suitable for baskets and is very easy to cultivate.

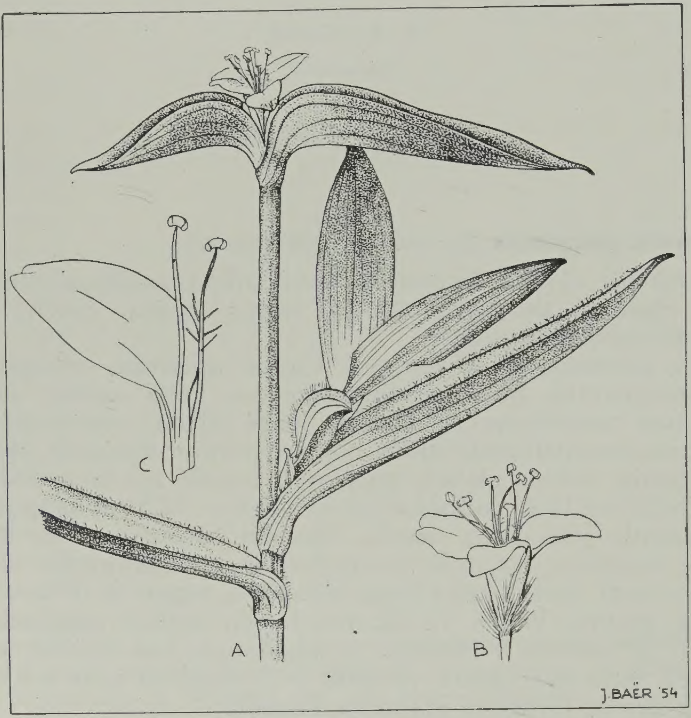

Fig. 1. SETCREASEA PURPUREA sp. nov.

Calathea makoyana Morr. in Belg. Hort., **23**, t. 24, 25, 1872 *(Marantaceae).*
Maranta makoyana Morr., l.c. pro syn.
Maranta olivaris Hort. Veitch ex Gardn. Chron., **1872**, 1589, f. 339.

This plant was discovered by E. Wittig, nurseryman at Rio de Janeiro and introduced into cultivation by Jacob-Makoy at Liege in 1871. As far as I know the flowers have never been described and the taxonomic position is still uncertain. Morren's opinion was that the plant should be related to *C. lindeniana* or *C. veitchiana.* In October 1954 the plant flowered in our glasshouse and I am now able to give the diagnosis of the flowering plant.

C. makoyana belongs to the subgenus *Microcephalum* Benth., the inflorescence being small and containing not more than 5 bracts. The scape bears one leaf, which corresponds to the other species of the subgenus. The diagnosis of this species has to be completed as follows: Acaulis. Spica ad 4 cm longa, pedunculo ad 10 cm longo, villosulo, apice ± incrassato, basi folio comitata. Bracteae 3–5, spiraliter dispositae, ovatae, villosulae, albomarginatae, inferiores apice cuspidatae, ± recurvatae, superiores apice acutae vel acuminatae. Paria florum 2, bracteolis hyalinis, mesophyllis setaceis comitata. Sepala lineari-lanceolata, 11–13 mm longa. Corollae albae tubus 15 mm longus, lobi lineari-lanceolati, 10 mm longi. Staminodium exterius 8–10 mm longus. Cucullatum 7 mm longum. Capsula?

Calathea lancifolia nom. nov. (*Marantaceae*).

C. insignis Bull, Cat., 1905, 2, non Petersen, 1890
Maranta insignis Ward in Gardn. Chron., **1906**, 1, 133.

This beautiful plant is still in cultivation; the flowers are unknown and the taxonomic position is therefore uncertain.

Crassula mesembryanthemoides (Haw.) D. Dietr., Syn. Pl., **2**, 1031, 1840 non Schönl. & Bak. f. (1902) (*Crassulaceae*).

Globulea mesembryanthemoides Haw. in Phil. Mag., **64**, 189, 1824 ("*mesembryanthoides*").
Sphaeritis paucifolia E. & Z., Enum., no. 1914, 1835.
Sphaeritis trachysantha E. & Z., l.c., no. 1915.
Crassula trachysantha (E. & Z.) Harv. in Harv. & Sond., Fl. cap., **2**, 362, 1862 et Hort.

There is no doubt that this plant, which is common in cultivation must bear this name, because D. Dietr. refers to the name of Haworth whose description of *Globulea mesembryanthoides* is clear.

Crassula corpusculariopsis nom. nov. (*Crassulaceae*).

Crassula mesembryanthemoides Schönl. & Bak. f. in Journ. of Bot., **40**, 284, 1902; Schönl. in Transact. Roy. Soc. S. Afr., **27**, 256, 1928 (1929) ("*mesembryanthoides*") non *C. mesembryanthemoides* D. Dietr. (1840) nec Dinter & Berger (1914).

Crassula dasyphylla Harv. in Harv. & Sond., Fl. cap., **2**, 355, 1862 (*Crassulaceae*).

Crassula simiana Schönl. in Journ. Linn. Soc. (Bot.), **31**, 552, 1897.
Crassula corallina Hort. non Thbg.

This plant which is rather common in cultivation by amateurs, is always treated as identical with *C. corallina* Thbg. But in the diagnosis of THUNBERG it is stated that the roots should be fusiform and our plants are entirely destituted of such roots, these being thin and filiform. In herbaria I found specimens with and without fusiform roots representing the two species with well defined areals and in cultivation both are present though the last one is very rare.

C. dasyphylla: roots filiform; branches creeping and rooting at the nodes; leaves for 1/3 white (top) with rather large green points; petals expanded, later often reflexed, yellowish; East S. Africa.

Examined specimens: *Drège 6885* (type); Kew Gardens, 1901: *N. E. Brown* (plant sent by *MacOwan* from Matjesfontein); Wilgenbosfontein, 1909: *W. C. Worsdell*; Cradock division, 1932: *H. W. James 153*; Hanover, 1916: *F. A. Rogers 16374*; Mortiner: *L. Kensit 9314*.

C. corallina: roots fusiform, woody; branches procumbent, not rooting at the nodes; leaves for 2/3 white, with small brown, later green points; petals erect, white; Western S. Africa.

Examined specimen: Aus, 1929: *Dinter 6106*.

Crassula radicans (Haw.) D. Dietr., Syn. pl., **2**, 1031, 1840 (*Crassulaceae*).

Globulea radicans Haw. in Phil. Mag., **66**, 27, 1825.

Schönland in Transact. Roy. Soc. S. Afr., **27**, 271, 1928 (1929) says, that the original diagnosis of Haworth does not cover the plant, which is generally known under this name. But Schönland is in error; he cited the diagnosis of *Kleinia radicans* (Phil. Mag. Nov. 1823) in stead of *Crassula radicans* (Phil. Mag. 1825).

Cordyline australis (Forst.) Endl., Prodr. Fl. ins. Norf., 29, 1833, quoad basonym; Hook. f. in Gardn. Chron., **1860**, 702; in Bot. Mag. t. 5636, 1867 (not t. 2835) (*Liliaceae*).

Dracaena australis Forst., Prodr., 141, 1786.
Dracaenopsis australis (Forst.) Planch. in Fl. d. Serr., **6**, 132, 1850–1.
Cordyline indivisa Reg. in Gartenfl., **1859**, 331 non Kunth (1850).
Cordyline superbiens K. Koch in Wochenschrift, **1859**, 380.
Dracaenopsis calocoma H. Wendl. in Bot. Zeit., **17**, 277, 1859.
Cordyline calocoma Hort. ex Bak. in Journ. Linn. Soc. (Bot.), **14**, 542, 1875.

Cordyline obtecta (Grah.) Bak., l.c., 543 *(Liliaceae)*.

Cordyline australis Endl., l.c., quoad descr., tab., syn., excl. basonym.
Dracaena australis Hook. in Bot. Mag., t. 2835, 1828, not Forst. (1786).
Cordyline baueri Hook. f. in Gardn. Chron., **1860**, 762.

There is concerning these species still confusion in botanical gardens. As Hooker f. l.c. pointed out Endlicher described a plant collected by Baur on the Norfolk islands under the wrong name *Dracaena australis* Forst. this being a different species. The numerous garden varieties belong to *C. australis*, but in literature we find always Hook. f. as author. *C. obtecta* is rather common in botanical gardens and we find this plant under all the names mentioned above.

C. australis Endl. is indigenous to Australia and was introduced into cultivation in 1836 from New Zealand to Göttingen (Germany). This species has long and narrow leaves with 30–40 veins on each side; the top of the leaves is rather long-acuminate and the lower are strongly reflexed. The tepals are expanded and ± campanulate at the base; the inner tepals are minutely serrulate (under strong lens). One of the 3 bracteoles of each flower fascicle is larger and more acuminate; the 2 others are smaller and obtuse.

C. obtecta Bak. is indigenous to the Norfolk islands and was introduced in 1820 from the botanical gardens at Sydney to those of Edinburgh. This species had broader leaves with 20–25 veins on each side; the top of the leaves is acuminate, the lower leaves are spreading or a little reflexed. The tepals are more inclined, the apices more reflexed and the inner ones entire. The 3 bracteoles of each flower are ± equal in length.

Dracocephalum atlanticum nom. nov. (*Labiatae*).

Dracocephalum mairei Emberger in Bull. Soc. hist. nat. Afr. Nord, **21**, 112, 1930 non Lévl. (1914).

This nice, white-flowering plant is not uncommon in botanical gardens and figures in the various seed lists always as *D. mairei.*

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NOTES ON THE MARANTACEAE OF SURINAME

BY

A. M. E. JONKER-VERHOEF AND F. P. JONKER
(Botanical Museum and Herbarium, Utrecht)

(received February 15th, 1955)

The list of *Marantaceae* published by PULLE (1906) comprises 20 species belonging to 6 genera, the largest genus being *Calathea* with 8 species. It was found, however, that one of the species does not belong to the family: investigation of the type of *Calathea strobilifera* (Miq.) Koern., viz. Kegel 1469 [GOET], showed that it pertains to *Renealmia strobilifera* Poepp. et Endl. (*Zingiberaceae*). The record of another species, *Calathea allouia* (Aubl.) Lindl. appeared to be based on a misidentification: the collection Focke 893 cited under this name by PULLE (1906) belongs to *C. grandis* O. G. Peters. Later on PULLE (1909) recorded the occurrence of one species more of this family in Suriname, viz. *Myrosma polystachya* Pulle, a new species. Since then no further additions to the list of Suriname species have been published.

Our investigation of the Suriname material showed the occurrence of 33 species belonging to 8 genera. In the following pages a few taxonomic and phytogeographical remarks are made on some of these genera and species; they also contain the description of a new genus.

CALATHEA G. F. W. Mey.

As mentioned above we had to remove from PULLE's list two species: *Calathea allouia* (Aubl.) Lindl. and *C. strobilifera* (Miq.) Koern. To the remaining 6 species we are adding 6 other ones, recorded for the first time from Suriname, viz.:

1. *C. lutea* (Aubl.) Spreng., once collected by the Forestry Department in the Wilhelmina Mountains; it was already known from the West-Indian Islands and tropical America.
2. *C. legrelleana* Reg., already collected by Splitgerber in 1838 but overlooked by PULLE; since then two other collections have been added. This species has been recorded from Ecuador, Colombia and Amazonian Brazil.
3. *C. cyclophora* Baker, hitherto known only from British Guiana, but recently collected four times by Lanjouw and Lindeman in Suriname.

Our investigation of the material in the Paris herbarium showed that this species occurs in French Guiana too, where it was collected by Leprieur and by Richard.
4. *C. micans* (Kl.) Koern., known before from Nicaragua, Guatemala, French and British Guiana, Amazonian Brazil, Colombia and Peru. In our opinion *C. albicans* Brogn. ex K. Schum. = *C. micans* var. *robustior* Koern. is to be considered a synonym. Both taxa have been based on specimens of a somewhat more robust growth.
5. *C. ovata* (Nees et Mart.) Lindl., a species up till now known only from Brazil, Bahia. Tubers of this species were collected by GEIJSKES at Mt. Temomairem, Toemoek Hoemak Mts., Upper Litanie River, and brought to Paramaribo where they were planted in the garden of the Agricultural Experimental Station; flowering plants gathered there were studied by us. The tubers are said to be eaten by the Wama or Wayaré hoelé indians. The plants are known to them as "oeroewa" and to the Oajana indians as "pisoi". The Wama indians have no agriculture; the edible tubers are collected from the wild plants, see GEIJSKES (1942). It is remarkable that the species has never been reported from the area between southern Suriname and Ilheos, Bahia, where the type and the other material known up till now were collected.
6. *C. mansonis* Koern. This species known from Bolivia, Brazil and French Guiana was collected in Suriname already about a century ago by Dr Voltz, later on it was collected again. The Voltz collection was regarded by PULLE (1906) as belonging to *C. propinqua* (Poepp. et Endl.) Koern.; the two species, indeed, show a close resemblance. *C. mansonis* is more robust and its inflorescence is always borne by a scape, but the latter may be very short. The inflorescence of *C. propinqua* is always sessile. The flowers of *C. mansonis* are more conspicuously pilose and their corolla tube is circ. four times as wide as that of *C. propinqua*. The corolla tube of *C. propinqua* is more than twice as long as the petals; in *C. mansonis* it is but slightly longer than the petals. The latter are slightly wider in *C. propinqua*. *C. propinqua* is known also from Amazonian Brazil and French Guiana. We are inclined, but before more material is known do not yet feel entitled, to consider *C. mansonis* a variety of *C. propinqua*.

C. villosa Lindl., known from Panama, Costa Rica, Colombia, Venezuela, Amazonian Brazil and British Guiana, is to be expected in Suriname.

MARANTA L.

In the genus *Maranta* PULLE (1906) listed two species, viz. *M. arundinacea* L. and *M. divaricata* Roscoe. We are adding two more species:
1. *M. orbiculata* (Koern.) K. Schum., once collected in Suriname by Rombouts at the Upper Sipaliwini River. Before it had been collected in Brazil only.
2. *M. humilis* Aubl. This species was collected by J. and P. A. Florschütz in 1951 between Ebba top and Pakka Pakka, Saramacca

River. It was described from French Guiana by AUBLET (1775) and, as far as we know, not collected again afterwards, though it was cited by KLOTZSCH (1848) for British Guiana. The Florschütz collection, though more robust, is undoubtedly conspecific with the Aublet specimen; the latter was studied by us from the Rousseau herbarium, recently purchased by the Paris herbarium, vid. LANJOUW & UITTIEN (1940). As this species was unknown to K. SCHUMANN (1902), the last monographer of the family, we wish to state that it belongs to the subgenus *Koernickea* K. Schum. It shows a close affinity to *M. longipes* K. Schum., but differs by the presence of a petiole (between sheath and pulvinus), by the shorter peduncle and by the longer petals and staminodes. The number of floral bracts is in *M. humilis* always four and in *M. longipes* more than four.

MONOPHYLLANTHE K. Schum.

The only species of this genus, *M. oligophylla* K. Schum., once before collected, viz. by Sagot in French Guiana, appears to have been collected three times in Suriname: once by Hulk at the Upper Gran Rio and twice by J. and P. A. Florschütz, respectively on the Brownsberg and at the Avanavero falls, Kabalebo River. As comparison with our own description in the "Flora of Suriname" will show, neither the floral characters nor the morphology of the inflorescence were correctly described by K. SCHUMANN (1902), the author of the genus, but as the differences with its allies are still sufficiently marked, we have maintained it.

MYROSMA L. f. and **HYLAEANTHE** Jonk. et Jonk.

The type of the genus *Myrosma* originated from Suriname where it was collected by Dalberg. The genus is characterized by the structure of the outer whorl of the androecium, which consists of two staminodes, by its very short corolla tube and by the persistent, coriaceous floral bracts, which subtend two or more flower pairs.

PULLE (1909) described a new species from Suriname, *Myrosma polystachya* Pulle, characterized by its inflorescence. He stated that one of the two outer staminodes was very small or absent. This species was up till now not collected again in Suriname; as far as we know it has been collected once in French Guiana (Geay 855 [P]). In our investigation of the type material we failed to observe the second outer staminode. Moreover we observed a striking resemblance in flower structure, in general habit and in the way in which the leaf sheaths decay into a reticulate mass of fibres, with *Myrosma hexantha* (Poepp. et Endl.) K. Schum., described by its authors in the genus *Thalia*, transferred by D. DIETRICH (1839) to *Maranta* and, by K. SCHUMANN (1902) in his monograph of the family, to *Myrosma*. The same holds for *Myrosma unilateralis* (Poepp. et Endl.) K. Schum. Both *M. hexantha* and *M. unilateralis*, originally described from Peru by POEPPIG and ENDLICHER (1838), appear to occur in Suriname too.

M. hexantha which is also known from Brazil, was collected at the Corantijne River by Hulk and in the Nassau Range by Lanjouw and Lindeman; *M. unilateralis*, known before from Peru only, was collected by the Forestry Department along Coppename creek, Lucie River, during the expedition to the Wilhelmina Mountains, 1926. The three species have chartaceous, oblong leaf blades, which are acuminate or apiculate at the apex and cuneate at the base. Their lower surface is light coloured and their margins are in herbarium material involute. Moreover the floral bracts are not coriaceous and the corolla tube is of the same length as the calyx or slightly shorter, but not, as in *Myrosma*, very short.

The generic limits of the genus *Myrosma* and several related genera are not always well defined and often inapplicable, as was pointed out also by WOODSON (1942), p. 333.

For all these reasons we feel entitled to unite *M. polystachya*, *M. hexantha*, *M. unilateralis*, as well as *M. hoffmannii* K. Schum. from Costa Rica into a new genus *Hylaeanthe*. We select *M. hexantha*, as it has been most often collected, as the type species.

Hylaeanthe Jonk. et Jonk., gen. nov. Folia rosulata, petiolo ad 2 cm longo instructa; pulvinus ad 6 mm longus; vagina membranacea ultimo in fibrillos reticulatos dissoluta; lamina chartacea, oblonga, subtus pallidior, basi cuneata, in sicco margine involutus. Bractaea herbacea. Paris florum pedunculati 3 vel ultra. Flores pedicellati; corollae tubus sepalis subaequilongus; staminodium exterius 1; staminodium cucullatum appendiculo pendulo obtuso instructum; stamen appendiculo petaloideo antheram superante munitum; ovarium imperfecte triloculare; loculus fertilis 1; ovulum basale solitarium.

Typus: *Hylaeanthe hexantha* (Poepp. et Endl.) Jonk. et Jonk. = *Thalia hexantha* Poepp. et Endl. = *Maranta hexantha* (Poepp. et Endl.) D. Dietr. = *Myrosma hexantha* (Poepp. et Endl.) K. Schum.

Species 4:

1. **Hylaeanthe hexantha** (Poepp. et Endl.) Jonk. et Jonk., vide supra.

2. **Hylaeanthe unilateralis** (Poepp. et Endl.) Jonk. et Jonk. = *Thalia unilateralis* Poepp. et Endl. = *Maranta unilateralis* (Poepp. et Endl.) D. Dietr. = *Saranthe unilateralis* (Poepp. et Endl.) Eichl. = *Myrosma unilateralis* (Poepp. et Endl.) K. Schum.

3. **Hylaeanthe hoffmannii** (K. Schum.) Jonk. et Jonk. = *Myrosma hoffmannii* K. Schum.

4. **Hylaeanthe polystachya** (Pulle) Jonk. et Jonk. = *Myrosma polystachya* Pulle.

We named the genus after the "hylaea" in which the species occur, adding the suffix "anthe" to bring it in accordance with similar generic names in the family e.g. *Ctenanthe*, *Saranthe*, *Stromanthe*.

THALIA L.

Pulle (1906) mentioned for Suriname a single species, *Thalia geniculata* L., known from tropical and subtropical America. Both Mr N. Y. Sandwith, Kew Herbarium, and Mr N. W. Simmonds, Trinidad, drew our attention to *Thalia trichocalyx*, described by Gagnepain (1904) from Mexico and French Guiana, from *T. geniculata* differing by shorter internodes between the floral bracts, much smaller flowers and floral bracts, sepals provided with long, slender, white hairs, and a horse-shoe-shaped aril.

According to Mr Simmonds *T. geniculata* is in the field easily distinguishable by its stouter, not taller, appearance and by the sterile bracts being red or purple beneath. In Trinidad both species grow together. After examining the material we quite agree with this distinction and we were much surprised to observe that most of the Suriname material belongs to *T. trichocalyx*. *T. geniculata* apparently does occur in Suriname, but this species has been collected only three times and that was a century ago (Splitgerber 169 [L], Kegel 603 [Goet], Hostmann 433 [K]).

ISCHNOSIPHON Koern.

Pulle (1906) mentioned 4 species, one of which, viz. *I. violaceus* Pulle, was described as new. The latter has been collected again by J. and P. A. Florschütz in 1951; up till now it is not recorded from other countries.

It is closely related to *I. martianus* Eichl., a less tall species, differing by the membranous margin of its leaf sheath which in herbarium material is chestnut-coloured, by its shorter leaf sheath, the very short or absent petiole, the shorter pulvinus, the more narrow and slightly shorter leaf blade, the much shorter peduncles and the slightly longer corolla tube. The latter species, known from Brazil and French Guiana, was recently for the first time collected in Suriname by Lindeman at Ricanau, Cottica River.

I. surinamensis (Miq.) Koern., cited by Pulle and by all monographers, is regarded by us as conspecific with *I. leucophaeus* (Poepp. et Endl.) Koern., known now from Panama, Guiana, Venezuela, Brazil and Peru. *I. ovatus* Koern. from Brazil is considered by us conspecific with *I. leucophaeus*.

Not mentioned by Pulle was *I. arouma* (Aubl.) Koern., already collected in Suriname in the 18th century by Rolander and after this collection several times from 1915 onwards. This species has been recorded from the West-Indian Islands, the Guianas and Brazil.

The *Ischnosiphon* species are known by the native indians under the vernacular name "warimbo" and other names. The splitted stems, especially of *I. gracilis* (Rudge) Koern., but also of *I. obliquus* (Rudge) Koern. and *I. arouma* (Aubl.) Koern., are used for basket weaving (Stahel, 1944).

MONOTAGMA K. Schum.

Of the four species listed by Pulle (1906) *M. laxum* (Poepp. et Endl.) K. Schum. was included because Kappler 1535 was identified as such, but this specimen appeared to belong to *M. plurispicatum* (Koern.) K. Schum. The genuine *M. laxum* was, however, collected in 1936 by H. E. Rombouts in Suriname at the Upper Sipaliwini River. This species differs from *M. plurispicatum* by the absence of the prominent ring at the base of the pulvinus.

Macbride (1931) pointed out that the well-known *M. parkeri* (Rosc.) K. Schum., also cited by Pulle, was conspecific with *Maranta spicata* of Aublet. Consequently the species has to be named *Monotagma spicatum* (Aubl.) Macbr.

Pulle (1906) described a new species, *M. surinamense* Pulle, that, in our opinion, is conspecific with *M. secundum* (Peters.) K. Schum.

As already suggested by Amshoff (1948) *M. guianense* (Koern.) K. Schum., described from French Guiana and cited by Pulle from Suriname, must be considered conspecific with M. *plurispicatum* (Koern.) K. Schum., described in the same publication (Koernicke, 1862) from Brazil, where the species has since then been collected several times. It seemed preferable to maintain the name *M. plurispicatum* (Koern.) K. Schum. as it is better known, and to consider *M. guianense* (Koern.) K. Schum. a synonym.

As representatives of this family may be of importance for characterizing vegetation units and as the plants do not always flower and as, moreover, the diagnostic characters are often distinguishable only by means of high magnifications, a key based on sterile material would, in our opinion, be desirable. Such a key has been given by Leonard and Mullenders (1950) for the species of Belgian Congo. The characters used by us for this key were derived from the habit, the kind of pubescence and the shape of the leaf blade, the length of pulvinus and petiole, etc.

1*a*. Plants provided with a single leaf (seldom 2 leaves); the latter oblanceolate to elliptical, 11–15.5 cm long and 2.5–5.5 cm wide; petiole and midrib pilose above. . . . . *Monophyllanthe oligophylla* K. Schum.
b. Plants provided with two or, usually, more leaves . . . 2
2*a*. Leaves arranged in a rosette at the top of a rather stout stem. 3
b. Leaves arranged in a radical rosette or along stem and branches 6
3*a*. Pulvinus glabrous. Midrib glabrous above. Leaf blade coriaceous, oblique, ovate, 27 – 46 cm long and 10 – 25 cm wide. . . . . *Ischnosiphon obliquus* (Rudge) Koern.
b. Pulvinus pilose above 4
4*a*. Leaf blade oblique, ovate, excentrically acuminate at the apex and rounded to truncate at the base, 20 – 51 cm long and 11 – 26 cm wide. . *Ischnosiphon arouma* (Aubl.) Koern.

b. Leaf blade almost symmetrical, elliptical, acute to cuneate at the base and acuminate at the apex. 5

5*a*. Leaf sheath coriaceous, 14.5–20 cm long; petiole 1.5–8 cm long; pulvinus 2–3 cm long; leaf blade up to 32 cm long and 9 cm wide. Plant 1–2 m high... *Ischnosiphon violaceus* Pulle

b. Leaf sheath 6–9 cm long; its margin membranous and, in herbarium material, chestnut-coloured; petiole up to 0.7 cm long or absent; pulvinus 0.7–1.5 cm long; leaf blade up to 26 cm long and 5,5 cm wide. Plant 60–80 cm high. . . . . *Ischnosiphon martianus* Eichl. ex Peters.

6*a*. Leafy and, sometimes, branched stems arising from a radical rosette 7

b. Leaves more or less arranged in a radical rosette; the latter occasionally reduced to one or two leaves; sometimes also with one or more leaves borne at the top of the scape. . . . 10

7*a*. Leaf blade oblique, lanceolate to ovate, 7–22 cm long and 4–9 cm wide, glaucous-pruinose beneath except a, 1 cm wide, green margin at one side, in herbarium material often chestnut-coloured beneath. Petiole usually absent. . . . . *Ischnosiphon gracilis* (Rudge) Koern.

b. Leaf blade symmetrical 8

8*a*. Leaf blade ovate, acuminate at the apex, rounded to truncate at the base, 15–31 cm long and 7.5–16.5 cm wide, glaucous-pruinose beneath. Pulvinus 1.5–3.5 cm long; petiole up to 34 cm long; leaf sheath 11–26 cm long . . . . *Ischnosiphon leucophaeus* (Poepp. & Endl.) Koern.

b. Leaf blade ovate-lanceolate, either attenuate, acuminate, or acute at the apex, rounded at the base. Pulvinus up to 11 mm long; petiole usually very short or absent but occasionally, in the leaves of the rosette, up to 1 cm long; leaf sheath up to 40 cm long 9

9*a*. Sheath and petiole pilose, glabrescent; pulvinus densely pilose. Leaf blade slightly pilose along the midrib, 6–28 cm long and 5–8 cm wide. Rhizome swollen (arrowroot) . . . . *Maranta arundinacea* L.

b. Sheath sparsely pilose; petiole usually absent; pulvinus pilose above. Leaf blade glabrous, 7–24 cm long and 2–12 cm wide; midrib slightly pilose at the base beneath. Rhizome not swollen . . . . *Maranta divaricata* Rosc.

10*a*. Pulvinus provided with a prominent basal ring. 11

b. Pulvinus without basal ring. 13

11*a*. Leaf blade slightly oblique, ovate-lanceolate to elliptical, either acute at both ends or the apex slightly acuminate . . . . *Monotagma secundum* (Peters.) K. Schum.

b. Leaf blade distinctly oblique, ovate to ovate-lanceolate, rounded and contracted at the base, excentrically acuminate at the apex 12

12*a*. Pulvinus and midrib pilose above. Leaf blade pilose along the

margin, 14–55 cm long and 5–18 cm wide. . . . .
. . . . *Monotagma plurispicatum* (Koern.) K. Schum.

b. Pulvinus pubescent all around; midrib and margin of the leaf blade pilose in the apical half, glabrescent. Leaf blade 25–43 cm long and 9–18 cm wide. . . . .
. . . . *Monotagma spicatum* (Aubl.) Macbr.

13*a*. Pulvinus always longer than 3 cm. Stout, robust herbs . . . 14

b. Pulvinus usually shorter than 3 cm 19

14*a*. Joint pilose all around when young; midrib of the leaf blade pilose beneath. Leaf blade lanceolate, apiculate at the apex, rounded and acuminate at the base, 30–68 cm long and 12–25 cm wide . . . . *Calathea comosa* (L. f.) Lindl.

b. Pulvinus and midrib glabrous 15

15*a*. Leaf without sheath (see also *Calathea grandis* Peters.) Leaf blade elliptical, 30–41.5 cm long and 9–13.5 cm wide; basal part of the midrib pilose above. . *Calathea zingiberina* Koern.

b. Sheath present. Midrib glabrous 16

16*a*. Leaf blade ovate, 27–84 cm long 17

b. Leaf blade elliptical to lanceolate, up to 60 cm long 18

17*a*. Pulvinus 5–10 cm long; sheath unknown. Leaf blade ovate, rounded at the base and, sometimes, near the pulvinus shortly contracted, acute at the apex, 20–74 cm long and 12–26 cm wide . . . . *Calathea grandis* Peters.

b. Pulvinus 5.5–16 cm long; sheath circ. 38 cm long. Leaf blade ovate or obovate, rounded at the base and near the pulvinus shortly contracted, rounded to obtuse at the apex, 27–150 cm long and 19–60 cm wide. .*Calathea lutea* (Aubl.) Spreng.

18*a*. Leaf blade elliptical, 23–60 cm long and 10–26 cm wide. Leaf sheath puberulous. . *Calathea elliptica* (Rosc.) K. Schum.

b. Leaf blade elliptical to lanceolate, 26–55 cm long and 7–22 cm wide. Leaf sheath provided with appressed hairs. . . .
. . . .*Calathea altissima* (Poepp. & Endl.) Koern.

19*a*. Pulvinus always shorter than 1 cm 20

b. Pulvinus (0.5) 1–3 cm long 27

20*a*. Leaf sheath leaving a rest of reticulated fibres when decayed. Petiole either absent or up to 1.5 cm long. Leaf blade chartaceous, cuneate at the base, light coloured beneath; margin involute in herbarium material. 21

b. Leaf sheath not leaving a rest of reticulated fibres. 23

21*a*. Leaf blade glabrous, elliptical, 13–30 cm long and 3.5–7 cm wide, acuminate at the apex; sheath 5–28 cm long. . . . .
. . . . . . *Hylaeanthe polystachya* (Pulle) Jonk. & Jonk.

b. Leaf blade oblanceolate or, sometimes, obovate, 6–11.5 cm wide 22

22*a*. Leaf blade glabrous, oblanceolate, 20–45 cm long, distinctly apiculate at the apex. . . . .
. . *Hylaeanthe hexantha* (Poepp. & Endl.) Jonk. & Jonk.

b. Leaf blade oblanceolate to obovate, 20–25(36) cm long, usually wider and shorter than in the preceding species, not or slightly apiculate at the apex; midrib and some of the lateral veins pilose. . . . . *Hylaeanthe unilateralis* (Poepp. & Endl.) Jonk. & Jonk.

23*a*. Petiole pilose above. Leaf blade falcate, elliptical, acute at both ends, 3–14 cm long and 1.5–4.5 cm wide. Leaf sheath 2.5–12 cm long; petiole 0.3–14 cm long. *Calathea micans* (Klotzsch) Koern.

b. Leaf blade not falcate, usually larger 24

24*a*. Leaf blade elliptical 25

b. Leaf blade obovate 26

25*a*. Leaf blade 8.5–14.5 cm long and 3.5 cm wide, acuminate at the apex and acute at the base, pilose on both surfaces, glabrescent above. Leaf sheath glabrous, 2.5–15 cm long; petiole 0–6 cm long, densely pilose above. . . . . *Myrosma cannifolia* L. f.

b. Leaf blade 8.5–24 cm long and 5–10 cm wide, rounded and acuminate at the apex, rounded at the base; midrib pilose. Leaf sheath sparsely pilose, 7–23 cm long; petiole 0.1–12.5 cm long, glabrous; pulvinus pilose above. . . . . *Maranta humilis* Aubl.

26*a*. Leaf sheaths and cataphylls densely golden-brown at the base; sheath 7–21 cm long; petiole 0–20 cm long, glabrous; pulvinus pilose above. Leaf blade elliptical to oblanceolate, oblique, acuminate at the apex, either rounded or acute at the base, 13–27 cm long and 4–11.5 cm wide, glabrous above, appressed pilose beneath. . . . . *Calathea mansonis* Koern.

b. Leaf sheaths and cataphylls not as densely pilose as in the preceding species. Sheath 3–16 cm long; petiole 0–10 cm long, pilose; pulvinus pilose above. Leaf blade oblanceolate, acuminate to apiculate at the apex and acute to cuneate at the base, 6–33 cm long and 3–14 cm wide. . . . . *Calathea propinqua* (Poepp. & Endl.) Koern.

27*a*. Pulvinus glabrous 28

b. Pulvinus pilose 30

28*a*. Leaf blade subcoriaceous, suborbiculate to broadly elliptical, rounded and excentrically acuminate at the apex and rounded or subacute at the base, 16–27 cm long and 10–20 cm wide, pilose at the apex above. Petiole usually absent but occasionally up to 6 mm long; leaf sheath 12–17.5 cm long, more or less bi-auriculate at the apex, subcoriaceous . . . . *Maranta orbiculata* (Koern.) K. Schum.

b. Leaf blade ovate-lanceolate, acute or acuminate at the apex, rounded at the base, glabrous 29

29*a*. Bracts subtending the inflorescence branches red or purple beneath and green and waxy above, up to 16 cm long. Petiole glabrous, 7–25 cm long. Leaf blade 38–60 cm long and up to 20 cm wide. . . . . *Thalia geniculata* L.

b. Bracts subtending the inflorescence branches green, up to 40 cm long. Petiole up to 23 cm long. Leaf blade 26–58 cm long and 5.5–24 cm wide . . . . . *Thalia trichocalyx* Gagnep.

30*a*. Pulvinus pilose all around, hirsute above; petiole puberulous, 16–34 cm long; leaf sheath 7–19 cm long. Leaf blade elliptical, distinctly oblique, maculate above, blue-purple beneath, 13–33 cm long and 10–17 cm wide; midrib glabrous above, puberulous beneath . . . . . . *Calathea legrelleana* Reg.

b. Pulvinus pilose above 31

31*a*. Leaf blade herbaceous, elliptical, nearly symmetrical, cuneate at the base and cuspidate at the apex, 14–34 cm long and 4.5–8 cm wide, pilose above, glabrous beneath. Leaf sheath pilose, 16–22 cm long; petiole usually absent. Tubers echinate, edible . . . . . . *Calathea ovata* (Nees & Mart.) Lindl.

b. Leaf blade usually rounded at the base 32

32*a*. Leaf blade herbaceous, oblique, elliptical, glabrous, acuminate at the apex and either acute or rounded and contracted at the base, 23–39 cm long and 7–13.5 cm wide, marked with an irregular, light green central zone above, brown purple beneath. Petiole glabrous, 11–57 cm long; leaf sheath 6–17 cm long, herbaceous. . . . . . *Calathea cyclophora* Baker

b. Leaf blade coriaceous, distinctly oblique, lanceolate or semi-ovate, shining above, excentrically and obtusely apiculate at the apex, rounded to truncate at the base, 30–43 cm long and 9.5–16.5 cm wide. Petiole absent in the leaf that subtends the inflorescence; its leaf sheath circ. 8 cm long . . . . *Monotagma laxum* (Poepp. & Endl.) K. Schum.

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OBSERVATIONS ON THE PROLIFERATION OF STEM PITH PARENCHYMA IN VITRO

I. General Introduction

BY

W. K. H. KARSTENS
(*Botanical Laboratory, Leiden, The Netherlands.*)

(*received March 8th, 1955*)

INTRODUCTION

The work of Gautheret (1935, 1939) and some of his collaborator, (e.g. Morel, 1948) has shown that cambium and its derivativels for instance xylem and phloem parenchyma elements, are suitabe for cultivation in vitro.

On the other hand White (1939 *a* and *b*) has proved that tumour tissue taken from a *Nicotiana*-hybrid is also able to thrive in vitro.

The work of these authors clearly shows that the internal structure of the cultivated products is, as a rule, a complex one, a not very surprising fact since cambium is destined to produce different types of cells. Furthermore, from the beginning both cambium and White's tobacco tumour tissue exhibited a certain complexity. The tissue cultures derived from such material show a disorderly arrangement of phloem and xylem elements embedded in parenchyma that is traversed by meristematic zones. In only a few cases a tissue culture consisting solely of parenchymatous cells has been derived from cambium (Gautheret, oral communication, Morel, 1948). In our own laboratory such a tissue culture has been obtained from a cambium proliferation of *Rosa banksiopsis* Bak.

It is perhaps advisable to discuss the term "differentiation". Weiss (1949) defines differentiation as the "unidirectional changes in the character of cells and cell generations during their life history, transformations by which they become increasingly different from their former selves, their parent cells, and the cells of other strains which have taken divergent courses". In this way differentiation is "unidirectional, progressive, and irreversible".

It is certainly not our intention to use the term differentiation in this sense. As a matter of fact, it is still quite questionable whether any plant cells exist which show differentiation in the way Weiss defines this for vertebrate cells, the more so where this author connects the occurrence of differentiation with the impossibility of dedifferentiation, "the actual return to a state of wider potency, i.e. the recuperation of something that had ostensibly been lost".

For plant cells Buvat (1944, 1945, 1951) describes a physiological differentiation followed by a morphological one, i.e. the formation of metabolic products, loss of activity to proliferate and reduction leading, finally, to extinction of histogenetical potentialities. According to Buvat dedifferenciation is possible. It is "le processus inverse de la différenciation, c'est un rajeunissement des cellules, qui leur fait recouvrir cequ'elles avaient perdu en se différenciant".

In order to solve the problem which of the definitions of the term "differentiation" applies it might be useful to have the disposal of strains of simple structure.

As mentioned before most plant tissue cultures exhibit a more or less complicated structure, even the parenchymatous strain of *Vitis vinifera* L. described by Morel (1948) contains many tannin cells amidst tannin-free ones.

The first thing to do was to try to find some plant tissue suitable as a starting material. It was considered possible that a simple tissue might proliferate to give a strain with a similar structure. Pith parenchyma was chosen, first of all because the medulla of many plant stems has a simple structure. Secondly, medullar parenchyma might breed true, while this tissue "shows up" nearest to the apex, and therefore, might have lost a number of potencies.

On the other hand several plants show certain idioblasts in the pith dispersed between the "normal" cells. Proliferation of this type of medulla might give some information about differentiation in the sense Weiss implies.

Scott (1941) studied the ontogeny of the stem of *Ricinus communis* L. In this plant several types of idioblasts occur, e.g. cells containing druses of calcium oxalate and so-called fat idioblasts. These idioblasts are arranged in longer or shorter vertical rows, indicating that the cells of each row were sooner or later derived from one idioblast mother cell. Bloch (1947) points out that the cells in question seem to have differentiated into a fixed state as they prove to breed true in wound tissue.

There remains the possibility that medullar parenchyma cells, as has been described for other cell types, have lost none of their potencies during the development of the stem and have retained the ability to dedifferentiate to a more or less meristematic state from which a variety of cells or tissues or even organs such as shoots or roots may arise (cf. Bloch, 1941, 1944; Buvat, 1944, 1945, 1951; Hartsema, 1926; Naylor and Johnson, 1937; Priestley and Swingle, 1929; Sinnott and Bloch, 1940). Simon (1908) describes proliferation of pith followed by differentiation into parenchymatous and lignified elements in cuttings of *Populus*. Úlehla (1928) mentions the appearance of new cell walls in discs of pith parenchyma of the giant cactus *Carnegiea gigantea* Britton and Rose which had been kept for three weeks on sucrose solutions. White (1939*a*), however, did not obtain any growth in excised fragments of medullary parenchyma of tobacco.

KANDLER (1950) mentions the proliferation of pith parenchyma of stem segments of *Impatiens*; details about the internal structure of these outgrowths are not given. It is necessary to lay stress on the fact that in the experiments of Simon and Kandler the pith cells remained in organic contact with the cells of the surrounding tissues. GAUTHERET (1951) mentions the proliferation of medullary parenchyma of the rhizome of the Jerusalem Artichoke resulting in the formation of callus containing vascular elements. It is not clear, however, whether isolated parenchyma tissue without attached vascular tissues was used by the author. JABLONSKI and SKOOG (1954), finally, using high concentrations of indole acetic acid (2–3 mg/l) failed to obtain cell division in excised tobacco pith. Cell division occurred, however, in pith tissue with attached vascular strands, in severed pith tissue placed in contact with vascular tissues, or even in isolated pith parenchyma if water extracts of vascular tissues are added to the nutritive medium. The same is the case with coconut milk or malt extract. In the presence of these substances callus formation was obtained. The tissue thus obtained can be maintained indefinitely in subcultures, and is capable of differentiation to produce vascular strands.

At the moment we started our investigation the publications of Gautheret and of Skoog and his collaborator had not yet appeared. However, the results obtained seem to us sufficiently important to justify their publication.

MATERIAL AND METHODS

A number of plants were studied with regards to the presence of a well-developed and living pith body. Only some of these plants, however, proved to possess pith that, under the studied circumstances, could be successfully cultivated in vitro.

Very appropriate for the purpose were medullary parenchyma from the stem of the Jerusalem Artichoke (*Helianthus tuberosus* L.), in an unknown variety and in the variety White Jerusalem Artichoke, and from suckers of the Elder (*Sambucus nigra* L.) and its weeping variety *pendula* Dipp. Furthermore, the stem of a garden variety of *Zinnia elegans* Jacq., the long shoots of *Ginkgo biloba* L. and twigs of *Taxus baccata* L. var. *aurea* Carr. furnished pith that, proliferating in vitro, produced results worth mentioning.

To isolate sterile medullary parenchyma, the stems and twigs are defoliated and debudded, then firmly rubbed with a wad of absorbent cotton wool soaked in alcohol 96 %, and for about one hour and a half, put into glass cylinders filled with a solution of chlorine and stoppered with absorbent cotton wool. The chlorine solution was prepared in the usual way by intermittently stirring during ten minutes of 100 gms of commercial bleaching powder with 1000 cc of tap water followed by filtration.

In the case of *Ginkgo* and *Taxus* the twigs show suberization. After desinfection with chlorine solution the bark is stripped off from the woody core and the thus peeled twigs are, in the usual way (MOREL, 1948), dipped into alcohol 96 % and washed twice with sterile water.

In the case of the remaining plants the herbaceous stems were treated with the chlorine solution and the outside layers, epidermis, cortex and pericambium, scraped off. Finally, the treated stems are rinsed with alcohol 96 % and sterile water as described before.

The twigs and stems thus prepared are cut under the protection of sterile filter paper into pieces of half an inch long. With the aid of specially made and sterilizable copper borers cylinders of medullary parenchyma can be punched out. The pith cylinders thus obtained can be pushed out of the borers by means of exactly fitting copper cores. The diameter of the isolated pith cylinders depends on the quantity of pith present in the stems and the twigs of the plants used. In the case of *Sambucus* the diameter of the cylinders measured 2.5–3.0 mm., in that of *Ginkgo* it amounted only to 1.0 mm.

After isolation the cylinders are transferred into culture tubes supplied with nutrient agar. Two methods to bring the cylinders into contact with the nutrient medium have been practised, either by laying them on the surface of the medium, or by sticking one end into the agar. As to the second method in the majority of cases the top end has been stuck into the medium, in some series both basal or distal ends were put into the agar. A more or less strongly expressed polarity of the pith cylinders could be observed.

In the case of *Taxus* a different procedure had to be followed. The twigs of this tree enclose a very narrow medullary core. With a suitable borer, diameter .65 mm., the pith can be punched out but no proliferation in vitro could be obtained. It is possible that relatively too many cells become injured to allow proliferation. In this particular case proliferation of pith could be obtained by sticking pieces of twigs of about 1.5 inch long, with the bark stripped off, into nutrient agar. Pith cells from the surface proliferate in a relatively short time to form a loosely adhering subglobose mass of cells. In view of the polarity the topend of the pieces has to be stuck into the medium.

Particulars about microtechnical methods will be given in the special parts.

SUMMARY

Plant tissue cultures exhibit in the majority of cases a diversity of cell types. This may be caused either by the complexity of the explanted material or by its potencies.

Only in a few cases tissue cultures have been obtained consisting of one type of cells. These cultures were derived from cambium. For the experimental approach of the problem of plant cell differentiation these simple tissue cultures may prove to be important.

It is conceivable that a simple tissue might breed true. This consideration and the fact that it differentiates very early in stem development led us to choose pith parenchyma as a starting material. It might have lost some of its potencies and have become more or less physiologically and morphologically fixed as seems to be the case with some types of idioblasts. This, however, proved not to be the case.

It is our intention to discuss the results obtained with the plants

investigated in a series of short papers. They will concern *Helianthus tuberosus* L. *Sambucus nigra* L. var. *pendula* Dipp., *Zinnia elegans* Jacq., *Ginkgo biloba* L. and the variety *aurea* Carr. of *Taxus baccata* L.

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OBSERVATIONS ON THE PROLIFERATION OF STEM PITH PARENCHYMA IN VITRO

II. THE INTERNAL STRUCTURE OF STEM PITH CYLINDERS OF *HELIANTHUS TUBEROSUS* L. CULTIVATED IN VITRO

BY

P. SEVENSTER AND W. K. H. KARSTENS
(*Botanical Laboratory, Leiden, The Netherlands*)

(*received March 8th, 1955*)

INTRODUCTION

The stem of the Jerusalem Artichoke, a typical short day plant, exhibits an intense vegetative growth during summer and early autumn. Flowerbuds in this country do not initiate before the end of September.

During the vegetative period the more robust stems show at their apical end living medullar parenchyma over a length of five to ten inches.

MATERIAL AND METHODS

The medullar parenchyma from stem tops sterilized on the outside can be easily punched out by means of sterilizable copper borers as described in Part I (Karstens, 1955). In this way cylinders of about 1.5 cm long and 2.5 mm in diameter could be obtained. They were cultivated at a temperature of 23° C in diffuse daylight in culture tubes with a nutrient medium of the following constitution: Knop's solution diluted by half with an addition of 1 gm/1 KC1 and 10 drops of a modified solution of Berthelot (Gautheret, 1942), glucose 20 gms, agar 10 gms, aneurin 1 mg, Ca-pantothenate 1 mg, inositol 100 mg, biotin .01 mg, cystein 10 mg, and α-naphtylacetic acid .5 mg per l. Later it was apparent that very simple culture media suffice for obtaining proliferation.

A certain number of cylinders were stuck into the medium, others were laid down upon the surface of the medium. In both cases a distinct polarity of the original material became clearly visible. Cylinders with their basal end (in relation to their original position in the intact stem) stuck into the medium showed proliferation only in the parts in direct contact with the culture medium or in its immediate neighbourhood. The top end remained unaltered.

When, however, the pith cylinders are stuck into the medium with their apical end, proliferation takes place over the whole length (Plate 1a). Dependent on the age of the explanted pith longitudinal growth may occur to a greater or lesser degree.

Plate 1b shows cylinders laid down flat upon the agar after five weeks of cultivation. If by irregular longitudinal growth the top end of the cylinder is lifted from the medium it will not show any proliferation at all and a smooth "tail" results. If, however, the basal part of the cylinder happens to be lifted from the medium, proliferation over the whole length results.

Cylinders were fixed directly after being punched out from the stem and at the end of five weeks of cultivation. As a fixative CRAF, consisting of a mixture of equal parts of chromic acid, glacial acetic acid and 10 % formol was used. After treatment with 70 % aethanol (three times during fifteen minutes) the material was dehydrated in four steps with butanol and embedded in paraffine (melting point 49° C). Sections 10 μ thick were cut, the paraffine was dissolved by means of xylene, and transferred to aethanol 50 %. The sections were stained in 1 % saffranin in 50 % aethanol during three hours, rinsed with aethanol 50 %, counterstained with a 1 % solution of fast green in an aethanol-xylene mixture 1 : 3. After rinsing with xylene the sections were mounted in balsam.

RESULTS

The untreated cylinders consist of longitudinal rows of parenchyma cells of uniform size, measuring around 100 μ in diameter and 50 μ in height. The outer surface shows the action of the borer; the cells are more or less damaged and have collapsed. In these cells the cell walls will show suberization in due time. Small intercellular spaces are present.

Details about the internal structure of one of the cylinders that has been cultivated during five weeks may follow here. In this case contact with the nutritive medium has been retained by means of basal part (Plate 1a). The basal part shows heavy proliferation slowing down to the smooth apical part. The total length of the explantate amounts to about one inch.

A short description of the anatomical structure of twelve equidistant transverse sections from a series of sections through part I of the explantate are given here (see Fig. 1).

Section 1. Sections through the smooth tail-end show no difference from the original pattern.

Section 2. At some distance from the end of the explantate the first symptoms of activity of the medullar cells become apparent. Some cells of the subsurface layer have divided by the formation of tangential cell walls. The division has taken place only in cells from that side of the explantate that was at some time in contact with the nutritive medium.

Section 3. The activity described above is perhaps somewhat greater in this section.

Section 4. Plate 2a shows that here the activity is much greater. Cells have divided by a repeated formation of tangential walls, thus forming a sort of meristematic zone. Later on cell walls in other directions have been formed. In this manner groups of cells are formed. Their joint origin from one and the same medullary cell is apparent. Some of the newly formed cells show a reticulate lignified cell wall. These cells are comparable with those described by SINNOTT and BLOCH (1945) and might be called tracheids. As before, the described activity is limited to that side of the explantate that was at some time in contact with the culture medium.

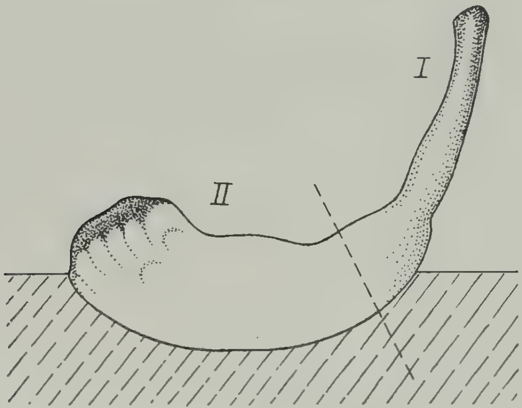

Fig. 1. Explanation see text.

The extreme surface layer consists mostly of cells that do not show any activity. At two points the suberized surface layer has been broken by small proliferations originating from cells of the sub-surface layers. The greater part of the section shows the original pattern, i.e. isodiametric cells with small intercellular spaces.

Section 5. The zone of activity extends along the surface. A few more tracheids are present. A new proliferation has broken the suberized surface layer.

Section 6. The extension of the zone of activity along the surface is much greater. Some groups of 6–9 tracheids or vessels are present, sometimes in transverse section, sometimes in longitudinal section, illustrating the bizarre course of these formations. On the distal side of the groups of tracheids some phloem elements can be found.

Section 7. The zone of activity has extended much more, in fact there is a nearly closed circular band of meristematic tissue present. A number of proliferations have broken through the surface layer and have partly merged into each other. In these areas the original borderlayer of collapsed cells lies amidst meristematic tissue. In the proliferations outside the original borderlayer scattered groups of vascular elements are present. Some scattered cells on the outmost border possess lignified reticulate cell walls (Plate 2b). In the meristematic band, present in a circle within the original borderlayer large groups of xylem and phloem elements have been differentiated. In general the phloem is orientated towards the outside of the explantate. The composing elements of these groups exhibit radial arrangement by the activity of a cambiumlike meristem (Plate 3a). The course, however, is, as has been mentioned, very irregular. The xylem elements when seen in longitudinal direction show beautiful perforation plates and may be called vessels. Within the just-described zone a core of non-modified medullary cells is still present. Similar cells, sometimes much enlarged, can be found between the vascular groups.

Section 8 and 9. The ring of vascular groups has lost something of its striking regularity by unequal development of its component groups.

Section 10. Many of the vascular groups undergo a continued radial expansion caused by cambial activity. The original borderlayer of collapsed cells is broken up more and more by the expansion of the underlying tissues. The cells of the sub-surface layer exhibit cell division by the formation of series of tangential walls, resulting in a second meristematic zone within the old margin of the explantate. Fig. 2 represents this stage.

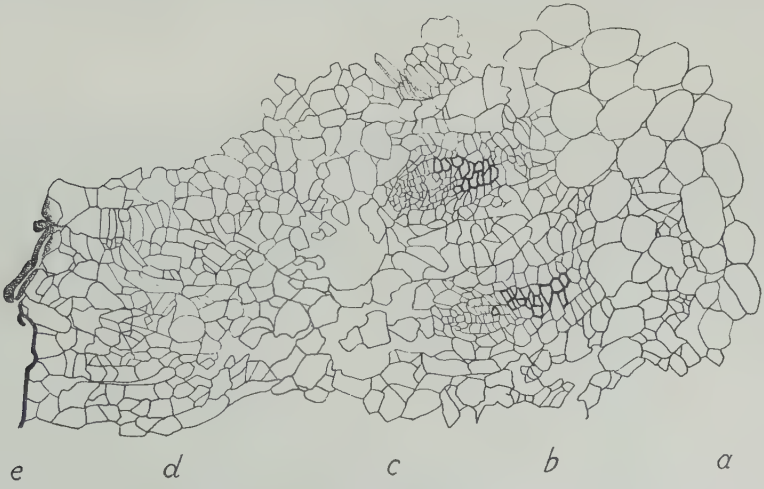

Fig. 2. *Helianthus tuberosus* L. *a.* Unchanged pith cells. *b.* zone with vascular groups. *c.* lacunae. *d.* meristematic zone. *e.* suberized margin. 65 ×.

Section 11 and 12 show the phenomena described in section 10 in a more pronounced way. The peripheral parts within the original borderlayer exhibit a great activity. The zone with the vascular groups undergoes distortion as the vascular groups expand in an irregular way. In the neighbourhood of these groups lacunae are formed by enlargement of intercellular spaces. Already in section 10 a few of such lacunae are to be found (Fig. 2).

The internal structure of Part II of the explantate (Fig. 1) is essentially very much alike that seen in section 12 of Part I. However, the situation distal to Part I becomes more and more chaotic. The vascular groups no longer show predominantly external phloem. They often have a very bizarre course (Plate 3b). In the centre of the explantate unaltered parenchyma cells are present in small scattered groups, the rest of them having undergone cell division.

DISCUSSION

From the above mentioned results it is obvious that the original hope that the medullar tissue from the stem might proliferate thereby producing a homogeneous tissue culture was not realised.

Pith cells prove able to dedifferentiate (Buvat, 1944, 1945, 1951). The process of dedifferentiation is accompanied by active cell division after which differentiation, one might call it redifferentiation, in different directions takes place. Vascular groups consisting of xylem and phloem elements are formed. A cambiumlike meristem is present.

At first a pronounced tendency for external phloem exists, later on this regularity is destroyed by irregular growth and very strange vascular groups and strands result.

Apart from the head-tail polarity a periphery-centre polarity appears to act which might be responsible for the observed phloem-xylem orientation. Further experiments are contemplated to elucidate this point.

ACKNOWLEDGEMENTS

Part of the apparatus used was purchased from a grant received from the Netherlands Organization for Purely Scientific Research (Z.W.O.)

We are very much indebted to Miss. E. van Wijnen (now Mrs E. van Die née van Wijnen) for making the photographs.

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P. SEVENSTER and W. K. H. KARSTENS: *II. The Internal Structure of Stem Pith Cylinders of Helianthus tuberosus* L.

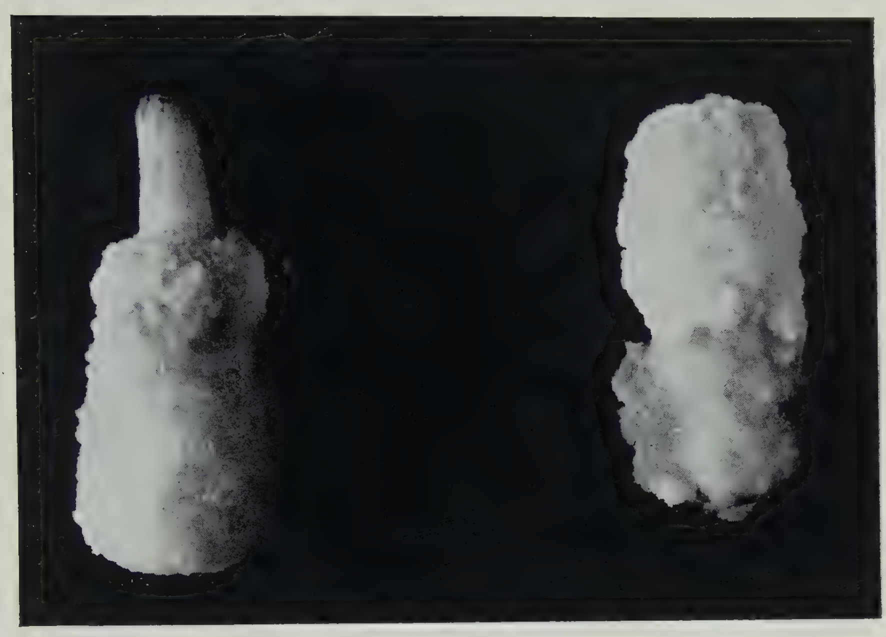

Plate 1a. *Helianthus tuberosus* L. Cylinders of stem pith after five weeks cultivation in vitro. Left: cultivated with basal end stuck into nutritive medium. Right: the same for the apical end. 3 ×.

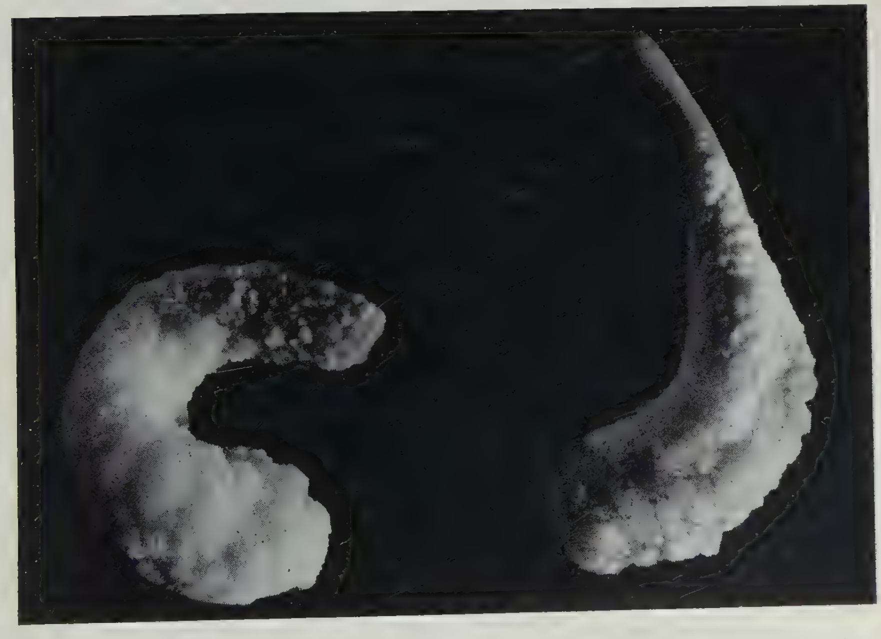

Plate 1b. *Helianthus tuberosus* L. Cylinders of stem pith after five weeks cultivation in vitro. Left: cultivated with apical end in contact with nutritive medium. Right: the same for the basal end. 3 ×.

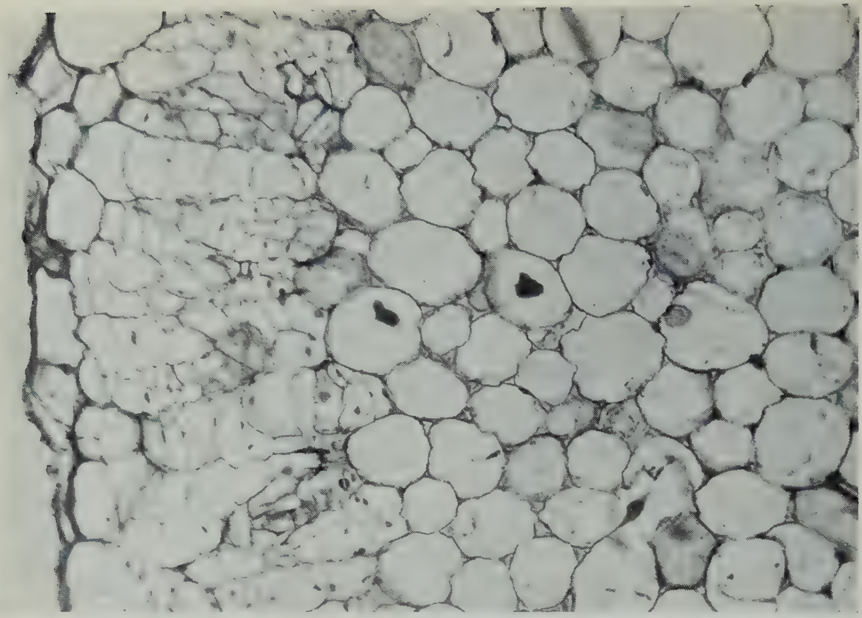

Plate 2a. *Helianthus tuberosus* L. Formation of a meristematic zone by the formation of tangential cell walls. The origin of the cell groups from medullary cells is obvious. A few tracheids are visible. Margin suberized. Considerable core of non-modified cells. 120 ×.

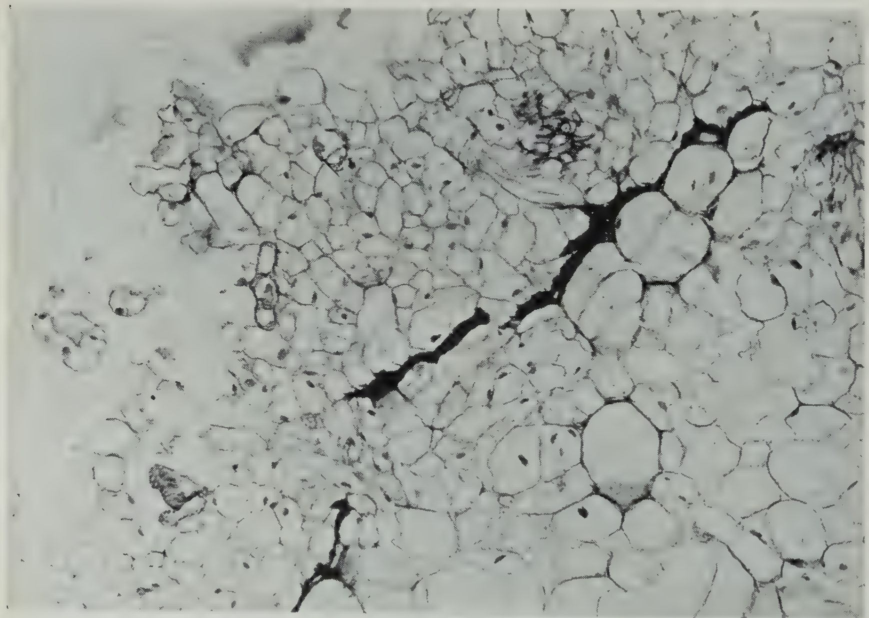

Plate 2b. *Helianthus tuberosus* L. The suberized margin is ruptured by proliferating cells, some of them are lignified. 100 ×.

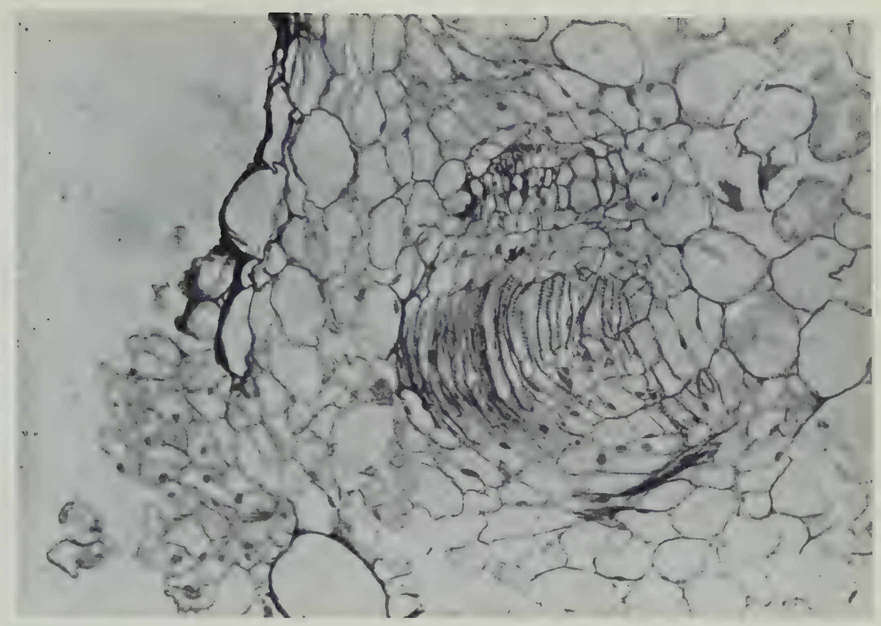

Plate 3a. *Helianthus tuberosus* L. A vascular group with external phloem and internal xylem, partly in longitudinal, partly in transverse section. Radial arrangement of the composing elements. Perforation plates in the xylem elements. 120 ×.

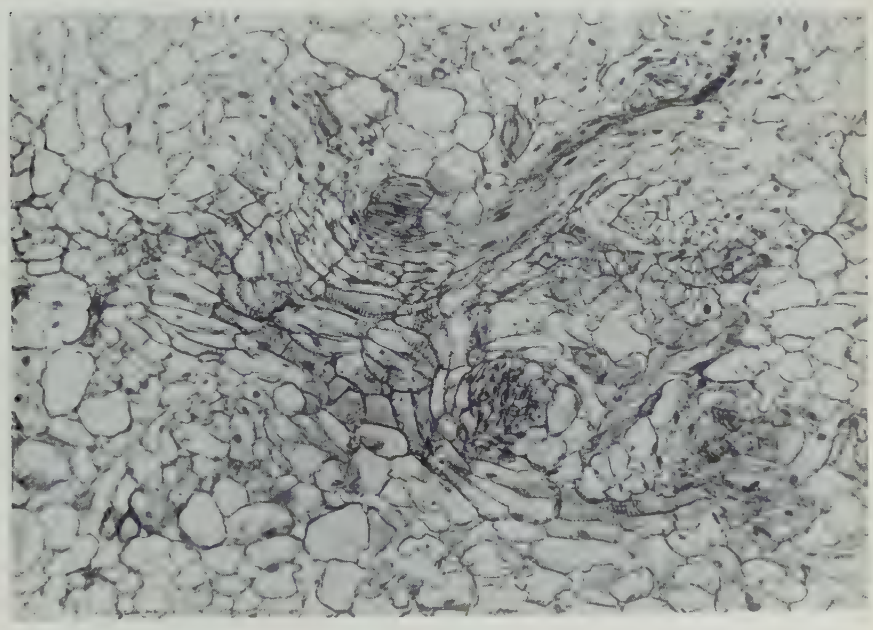

Plate 3b. *Helianthus tuberosus* L. Vascular groups and strands. Perforation plates. Remnants of the original medullary tissue still clearly visible. 65 ×.

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OBSERVATIONS ON THE PROLIFERATION OF STEM PITH PARENCHYMA IN VITRO

III. GROWTH AND DEVELOPMENT OF EXCISED STEM PITH CYLINDERS OF *SAMBUCUS NIGRA* L. VAR. *PENDULA* DIPP.

BY

C. A. CLAUSING (NÉE MELCHIOR) AND W. K. H. KARSTENS
(*Botanical Laboratory, Leiden, The Netherlands*)

(*received March 8th, 1955*)

INTRODUCTION

Apart from some introductory remarks it was announced in the first publication of this series (Karstens, 1955) that a.o. the proliferation of stem pith in vitro of the variety *pendula* Dipp. of *Sambucus nigra* L. would be described.

Although the anatomy of the untreated pith is very much alike that of the stem of *Helianthus tuberosus* L. the type of proliferation of *Sambucus* pith differs greatly from that of the Jerusalem Artichoke (Sevenster and Karstens, 1955).

MATERIAL AND METHODS

An old plant of the weeping variety of the Elder growing against the conservatory in the Botanic Garden furnished the material used in our experiments. Each spring the plant is cut back onto the old wood resulting in the growth of drooping suckers several yards long.

The material consisting of tops of suckers containing green active pith was treated as described before (Karstens, 1955). Pith cylinders of 1.5 cm length and with a diameter of 3 mm could be easily obtained and were put horizontally on nutritive agar. The constitution of the culture medium and further treatment are the same as described before (Sevenster and Karstens, 1955). This is also the case with fixation and sectioning of the material. For staining a combination of Delafield's haematoxylin, saffranin and fast green were used.

DESCRIPTION OF THE RESULTS

Seen in transverse section the freshly excised pith of *Sambucus* consists of more or less irregularly arranged multiangular parenchyma cells with small intercellular spaces. The longitudinal section shows, according to expectation, cells arranged in longitudinal rows. In the phase studied the cells measure 36–90 μ in width and 20–116 μ in length.

Plate 1a, first of all, illustrates proliferation of cylinders laid horizontally upon the culture medium and seen from above. A freshly excised cylinder is shown in (d), while (a) and (b) represent cylinders after about 20 and 40 days of cultivation resp.: (c), finally, shows a cylinder with the basal end stuck into the nutritive medium after 40 days cultivation.

After 20 days cultivation the upper surface of the excised cylinder is covered with very fine downy flocks, merging into a thin more or less continuous layer along the sides of the explantate and terminating in a shallow ridge on a level with the agar medium. Later on the whole surface of the cylinder becomes covered with a greenish white layer formed by fusion of individual proliferations. This process, however, proceeds at a different pace from one point to the other. Plate 1a (b) especially the top half of the figure illustrates this clearly. In the central part of the upper surface the process is strikingly quicker than at its extremities. It stands to reason that in the photograph the border of new tissue along the lines of contact with the nutritive medium is not visible. The cut ends, finally, show cushion-shaped masses of newly formed tissue.

As is the case with the excised pith of *Helianthus tuberosus* (SEVENSTER and KARSTENS, 1955) a very distincy polarity manifests itself. Plate 1a (c) represents an excised pith cylinder with the basal end stuck into the nutritive medium. Transport of stimulants from the medium only has taken place over a short distance. As with *Helianthus* a smooth non-proliferating "tail" results.

So far the difference with *Helianthus* does not seem very important. The study of the microscopical changes, however, reveals a fundamental difference.

While the pith parenchyma of the Jerusalem Artichoke becomes active through and through on cultivation, the pith cylinder of *Sambucus* shows a very limited activity in the interior, ending in necrosis. The relatively poorly developed proliferations on the outside of the Jerusalem Artichoke cylinders, furthermore, are in striking contrast with the huge quantity of new tissue in the case of *Sambucus*. Thus, for subcultures the whole mass of tissue can be used in the case of *Helianthus* while for *Sambucus* the new outgrowth has to be taken.

Some more information regarding the internal structure of pith explantates after different periods of cultivation can be given.

Fig. 1 illustrates the line along which the development takes place. In a schematical way transverse sections are presented which show a number of zones in a series of explantates cultivated for a longer or shorter time. No I represents the situation of a freshly excised cylinder in contact with the nutritive medium. Nos IIa and b represent schematical drawings of transverse sections of one of the extremities and of the central portion of an explantate cultivated during 25 days. Nos

C. A. CLAUSING (née Melchior) and W. K. H. KARSTENS: *III. Growth and Development of Excised Stem Pith Cylinders of Sambucus nigra* L. *var. pendula* Dipp.

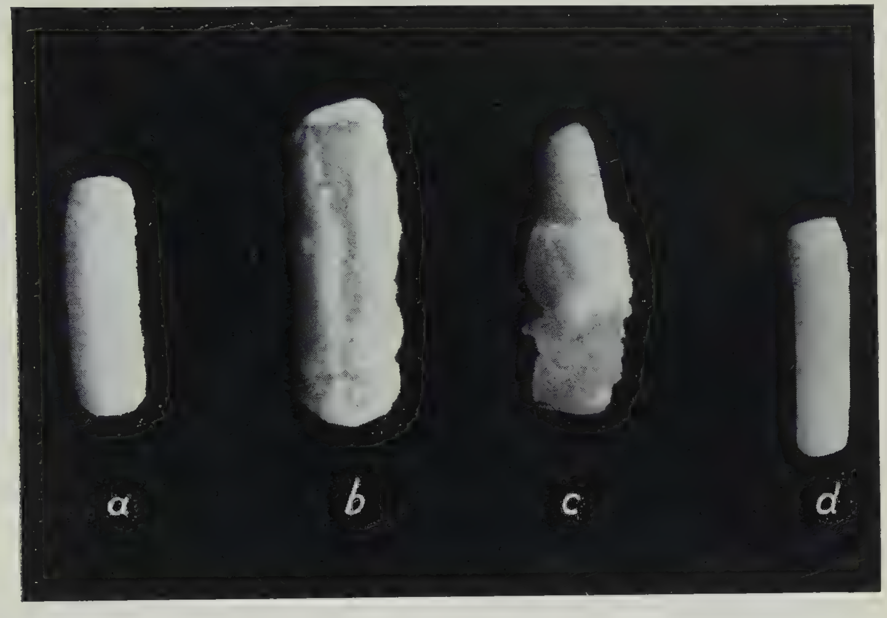

Plate 1a. *Sambucus nigra* var. *pendula*. Excised pith cylinders cultivated in vitro. (a) and (b) placed horizontally, 20 and 40 days cultivation resp., (c) stuck into culture medium with basal end after 40 days cultivation, (d) freshly excised cylinder. 1.7 ×.

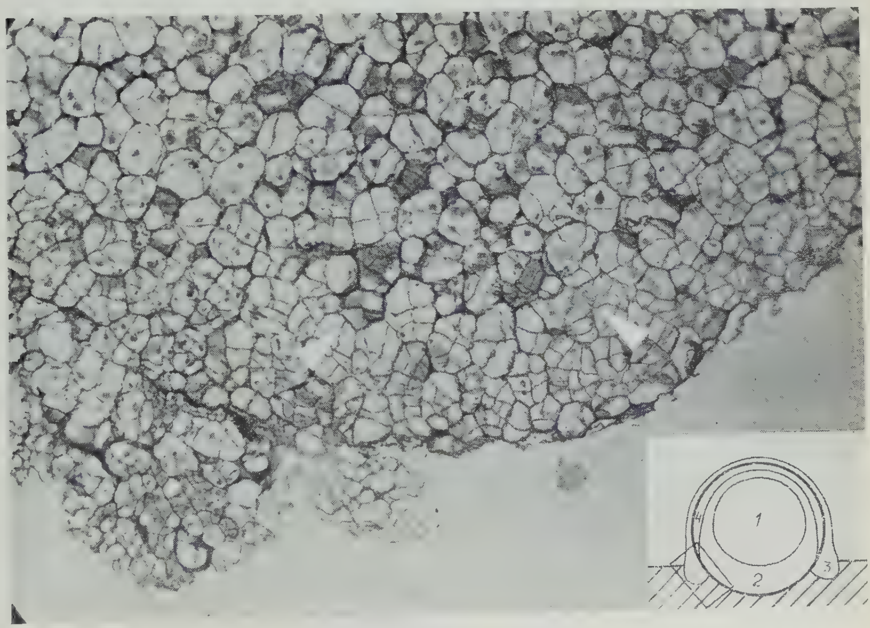

Plate 1b. *Sambucus nigra* var. *pendula*. Most medullary cells have divided more or less (2), the suberized borderline of the explantate is clearly visible as well as the new outgrowth (3). Some lignified cells are indicated by arrows. 50 ×.

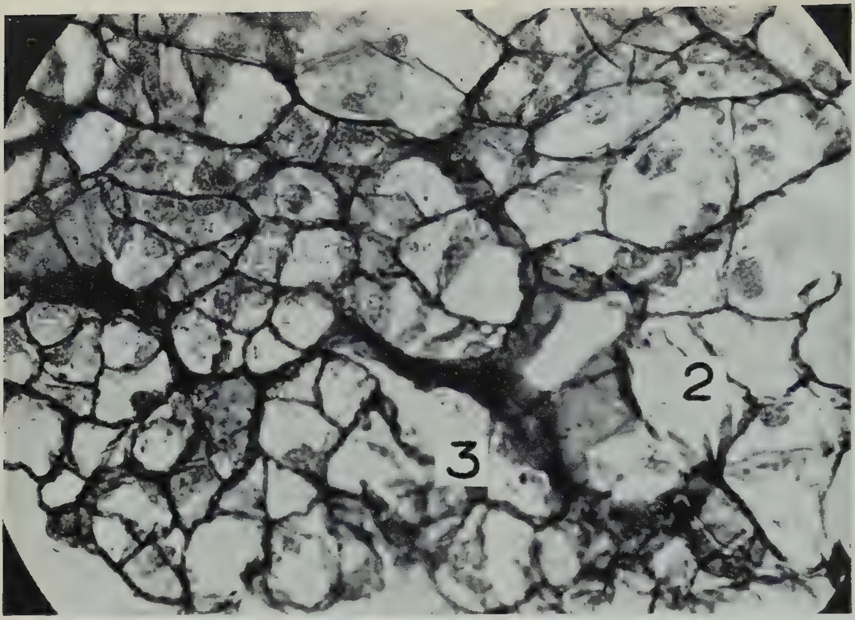

Plate 2a. *Sambucus nigra* var. *pendula*. Marginal groups of cells of zone 2 rupture the suberized border layer to contribute to the formation of zone 3. 200 ×.

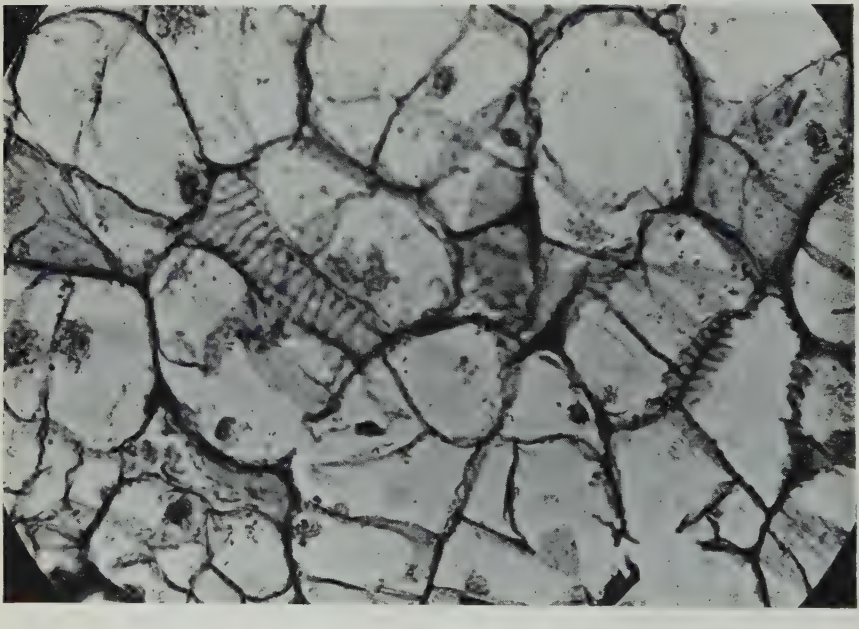

Plate 2b. *Sambucus nigra* var. *pendula*. Detail of zone 2. Medullary cells without losing the original shape have divided repeatedly. Some of the division products exhibit heavily lignified scalariform thickening of the cell wall. 225 ×.

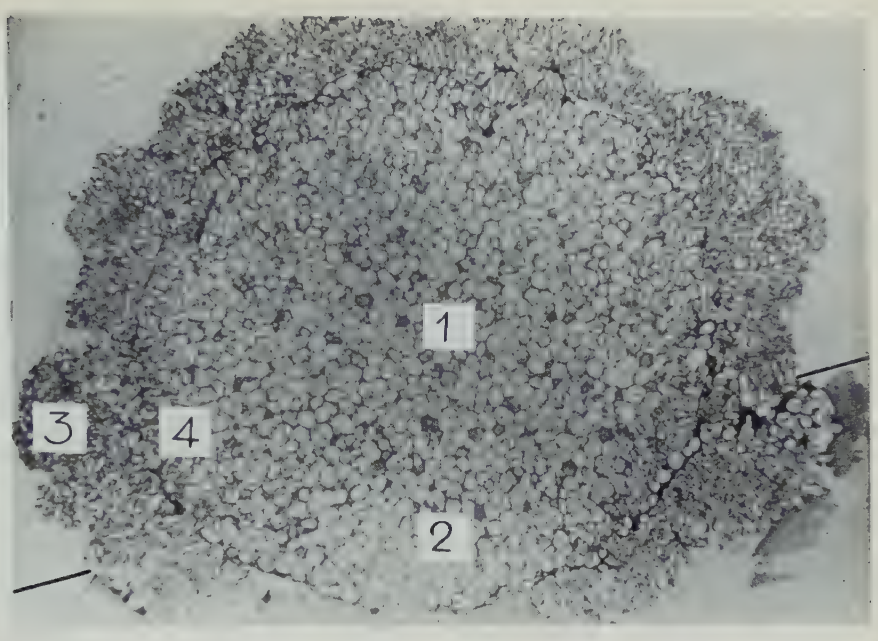

Plate 3a. *Sambucus nigra* var. *pendula*. Transverse section of a horizontally placed pith cylinder after 46 days of cultivation. Zones 1, 2, 3 and 4 are clearly visible. The heavy line indicates the border of the nutritive medium of which stained patches are discernable. 18 ×.

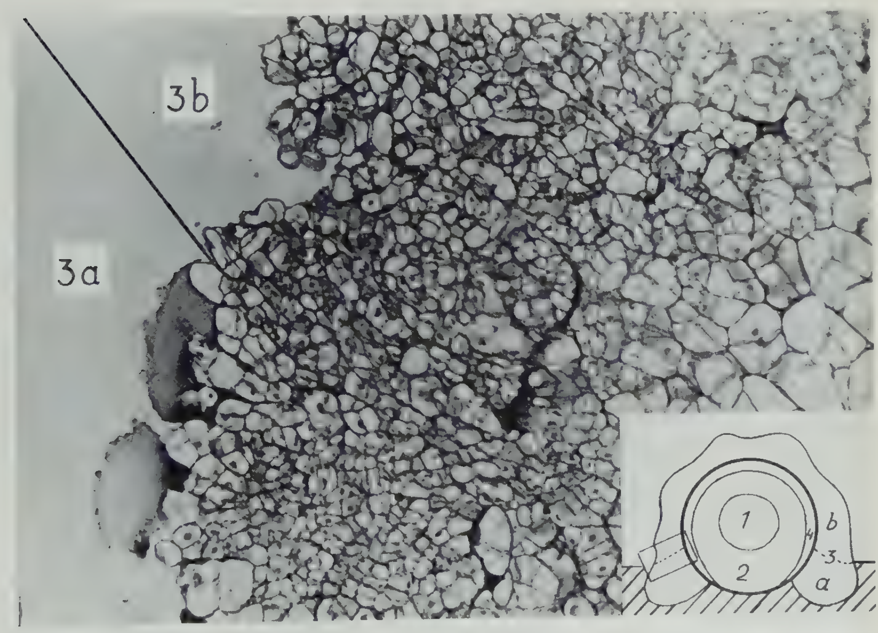

Plate 3b. *Sambucus nigra* var. *pendula*. Details of the proliferation zone (3); 3a pictures the proliferation in contact with the nutritive medium (stained patches visible), 3b shows the proliferations in the air. The heavy line indicates the partition between the two portions of (3). 50 ×.

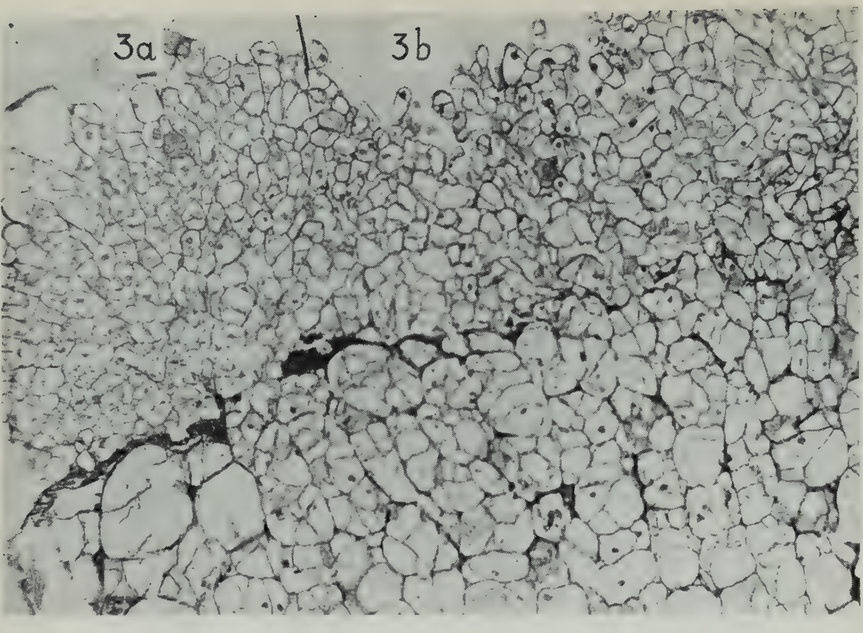

Plate 4a. *Sambucus nigra* var. *pendula*. Details of the proliferationzone (3); 3a shows a typical thin walled closely built fanlike proliferation in contact with the nutritive medium; 3b shows the thick walled loosely built outgrowth in contact with the air. 50 ×.

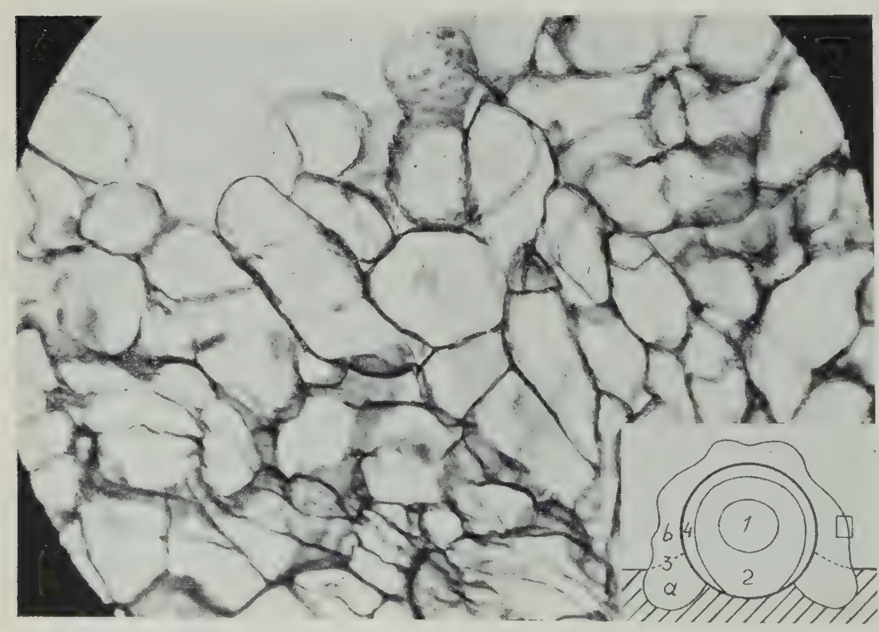

Plate 4b. *Sambucus nigra* var. *pendula*. Marginal cell (zone 3b) with pectic warts and reticulate lignification. 230 ×.

III and IV, finally, represent stages after 46 and 117 days of cultivation resp. Unchanged parenchymatous tissue is indicated with (1), while (2) represents a zone in which all or almost all cells have divided more or less, however, without loss of the original cell shape. In older explantates zone 2 exhibits the differentiation of a lateral meristem-like border, marked as (4), by the formation of a series of tangential cell walls. The areas 1, 2, and 4 are situated within the circumference of the original explantate, the borderline of which is indicated by a heavy line. Zone 3, finally, is produced by fusion of proliferations breaking through the original border. A distinction between 3a and 3b has to be made, indicating new growth in contact with the atmosphere and with the nutritive medium resp.

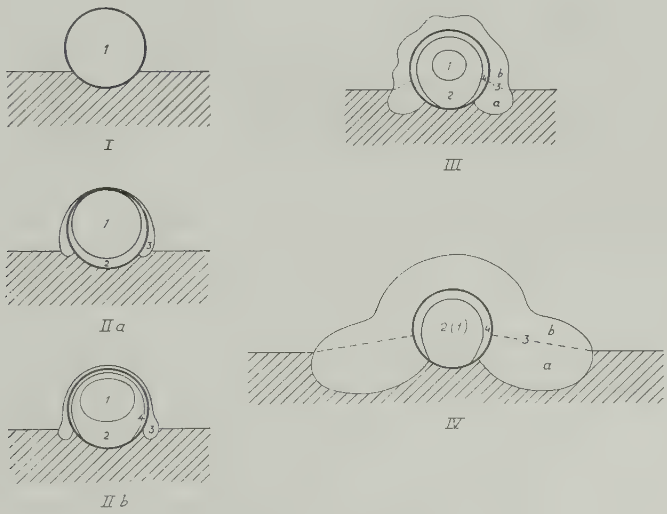

Fig. 1. Development of excised cylinders horizontally placed upon culture medium. Schematical representation of transverse sections. Culture medium hatched, border of the original explantate drawn with a heavy line. For further explanation, see text.

After having given this rough draft of the facts observed some details may follow here. Plates 1b, 2a, and 2b represent different parts of explantates which have been cultivated during 25 days. In Plate 1b part of the original explantate and a portion of the marginal proliferations can be recongized. The major part of the picture shows the split up cells of zone 2 (Fig. 1, IIa). To the left the still limited outgrowth of zone 3 on the border of the nutritive medium and atmosphere is apparent. In this part of the section the thick suberized outer layer of the original explantate has been ruptured by outgrowing cell groups (See also Plate 2a) Several cells of zone 2 show lignification in a scalariform pattern (Plate 2b). This same pattern is found in cells of the upper part of zone 3.

Fig. 1, III and Plate 3a show the gross structure of an explantate after 46 days of cultivation. Only a small portion of unchanged cells (zone 1) is left, the zones 2, 3, and 4, however, are much more developed than in the explantate cultivated for 25 days. The outline of the original cylinder remains visible, the diameter, however, has grown somewhat through the activity of zone 4. The greater part of the expansion of the whole system is due to the activity of zone 3. Apart from the heavy ridge in contact with the culture medium a 1 mm thick, small-celled layer of new tissue covers the explantate. The part of the lower side of the explantate between the collateral ridges shows no proliferation at all.

Zone 1, 2, and 4 do not exhibit new features, zone 3, however, shows some details worth mentioning.

First of all there exists a striking difference between the structure of the new tissue grown into the culture medium (Fig. 1, III, zone 3a) and that developed above the agar (zone 3b). Zone 3a (Plate 2b) consists of fan-like proliferations rupturing the thickened and suberized borderlayer of the explantate and forming a compact meristematic tissue. The marginal cells of the proliferations stretch out into the agar and divide. Their proximal division products come into close mutual contact and form a compact tissue that keeps its dividing activity: thus the proliferations may expand by two methods, i.e. by the pioneer action of the marginal cells and by the expansion caused by division of the cells of the adjoining tissue behind them. Differentiation does not occur in zone 3a.

As to zone 3b, some of the observed phenomena are comparable with those previously described for zone 3a; some, however, we have not met before.

As to the structure of the proliferations above the agar (zone 3b), a primary and a secundary phase çan be observed. The first phase is comparable to the state of affairs described for zone 3a. As a matter of fact, here again marginal cells are encountered stretched out into the surroundings, in this case the atmosphere. These marginal cells are often much longer than the corresponding elements of zone 3a. In addition the division products form a relatively loose and irregularly built tissue.

It is remarkable that contrast to our knowledge of the internal structure of plant tissue cultures, hardly anything is known about the methods by which a plant tissue culture expands on the outside. Gautheret (1942–43) describes the presence of longer or shorter, more or less branched chains of cells, arising from dividing cells scattered over the surface of many types of explantates cultivated in vitro to which he gave the name of "pseudo-thalles" because of the resemblance of the thallus of certain fungi. They have been described earlier by Magnus (1918) who gave these formations the name of "Wundhaare". Gautheret (1937) was at first of the opinion that these formations were comparable to the migrating cells of animal tissue cultures. The fact that the cell chains cannot be subcultured, which is in contrast with the recently described animal cells, led him to the conclusion that his former comparison was not longer allowable.

Gautheret's "pseudo-thalles" remain free; they never fuse. A substantial expansion of the explantate is, according to this author, only possible if the proliferation of cells "se généralise à toute la surface du tissu, dont toutes les cellules se multiplient: le fragment produit alors un parenchyme compact légèrement mamelonné que l'on pourrait interpréter comme étant formé d'une grande quantité de pseudo-thalles étroitement unis les uns aux autres."

Caplin (1947) investigated the way by which a cube cut out of a tobacco tissue culture grew in subculture. According to this author knobs of new tissue are formed in two ways. One way is by a process of cleavage caused by failure of a cell, or a row of cells, on the surface to continue dividing. Instead such cells enlarge greatly, while the surrounding cells continue to divide and give rise to new knobs. The other method is by the formation of groups of actively dividing cells in the subsurface of existing knobs. Tangential walls are formed and by increment or size of the newly formed cells the knob grows out with the cells in radially diverging rows, resulting in a fan-like structure when sectioned and fountain-like when seen in space. There was no mention of the activity of marginal cells although some of the figures of Caplin show their presence.

From the above it will be clear that our material behaved in a different way. Practically all cells just below the suberized skin at the margin of the explantate become active but only on a relatively small number of places the activity is such that the suberized skin becomes ruptured. From these points pseudo-thallus like and fan-like proliferations originate, together forming a sort of pseudo-parenchyma which gradually becomes more solid (Plate 4a).

In so far zone 3a and 3b present essentially the same picture, except that the cells of zone 3a are smaller (Plate 3b). However, in zone 3b changes occur at a certain moment. As a matter of fact, differentiation takes place in zone 3b, while zone 3a never shows any. As in zone 2 some elements exhibit lignified cell walls, some, as is the case in zone 2 (see Plate 2b,) of a scalariform pattern others of a reticulate lignification. Sometimes isolated marginal cells exhibit both pectic warts and a reticulate lignification (Plate 4b).

Another difference is the occurrence of cup-shaped or gutter-shaped cambial zones with matching internal xylem and external phloem elements (Plate 5a).

Finally, some remarks have to be made concerning a cylindrical pith explantate after having been cultivated for a period of 117 days.

Fig. 1, IV illustrates a continuation of the course of things observed in explantates of a younger age. This is specially true of the development of zone 3a and 3b.

In a certain sense the same is the case with the original explantate. The original medullary parenchyma e.g. has practically disappeared, here and there scattered remains are encountered.

The most spectacular difference, however, is a totally different orientation of the elements within the original and suberized borderline. In the explantates of 25 and 46 days cultivation more or less concentric changes have taken place in the old tissue (zones 1, 2, and 4). This is in complete agreement with the original stem pattern. After 117 days of cultivation this situation is fundamentally changed. A very distinct orientation towards the culture medium has manifested itself, resulting, as seen in transverse section, in a kind of peacock's tail (Plate 5b). A radiating structure originating from the bottom of the explantate results, presumably by expansion of composing cells along new axes. In addition, cell complexes in zone 4 have expanded in such a way that the suberized borderline has become undulated. In the central part groups of cells of a bizarre shape and with heavily lignified cell walls have been formed.

The original expansion of the explantate (see page 196) has probably undergone a regression by necrosis of the tissue, followed by inward expansion of zone 3. A free contraction from the nutritive medium has taken place in the bottom part of the explantate (Plate 5b).

DISCUSSION AND SUMMARY

The results obtained by cultivating excised medullary parenchyma of *Sambucus nigra* L. var. *pendula* Dipp. clearly indicate that the properties differ greatly from the corresponding tissue of the Jerusalem Artichoke, *Helianthus tuberosus* L. While in the case of *Helianthus* virtually the whole explantate proliferates by cell division and differentiation this proves not to be the case with *Sambucus*-pith. Here, on the contrary, growth of the explantate takes place exclusively through the formation of a considerable layer of new tissue on the outside of the explantate.

External factors have a profound influence on the structure of the newly formed tissue. Contact with the atmosphere results in a parenchymateous tissue consisting of small cells, some of them exhibiting scalariform or reticulate lignification. Furthermore, more or less cup-shaped formations consisting of internal xylem and external phloem arise from isolated cambial zones.

A complete contrast is provided by the structure of the new tissue that develops in contact with the nutritive medium. A homogeneous tissue consisting of thin walled non-differentiating cells results.

As to the original explantate, this retains its individuality. Even after 117 days of cultivation the dimensions have not changed considerably and the original borderline is still visible. The pattern of the explantate, however, has undergone a very striking transformation. As might be expected alterations take place according to the original radial pattern of the pith resulting in a number of concentric zones. After prolonged cultivation, however, presumably by expansion of the composing cells along induced axes a different structure, as seen in transverse section not unlike a peacock's tail, originates.

Finally, the original explantate dies off.

ACKNOWLEDGEMENTS

We are very much indebted to the Netherlands Organisation for Pure Research (Z.W.O.) for a grant used for purchasing part of the apparatus used.

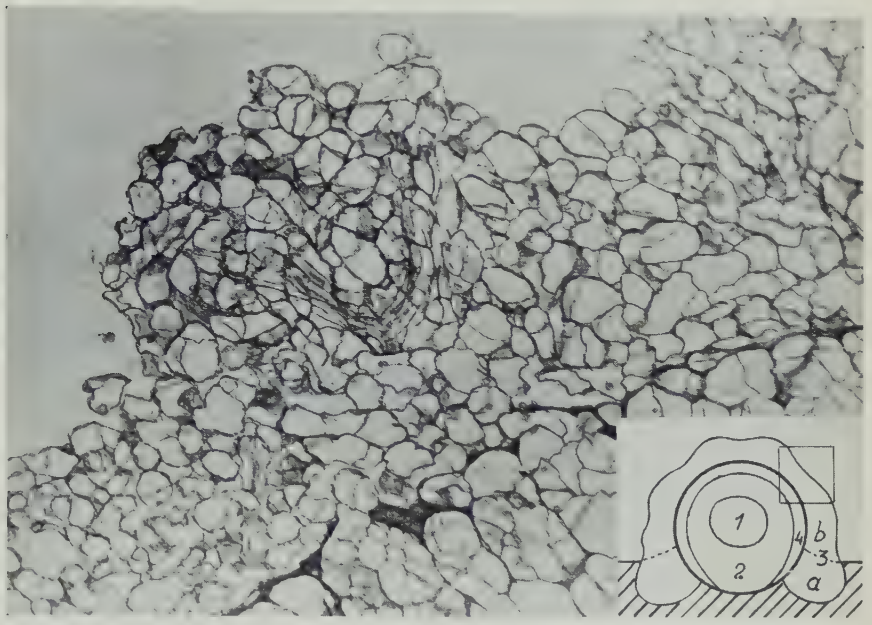

Plate 5a. *Sambucus nigra* var. *pendula*. Differentiation in (3b). A cambial zone with internal xylem and external phloem is present. 70 ×.

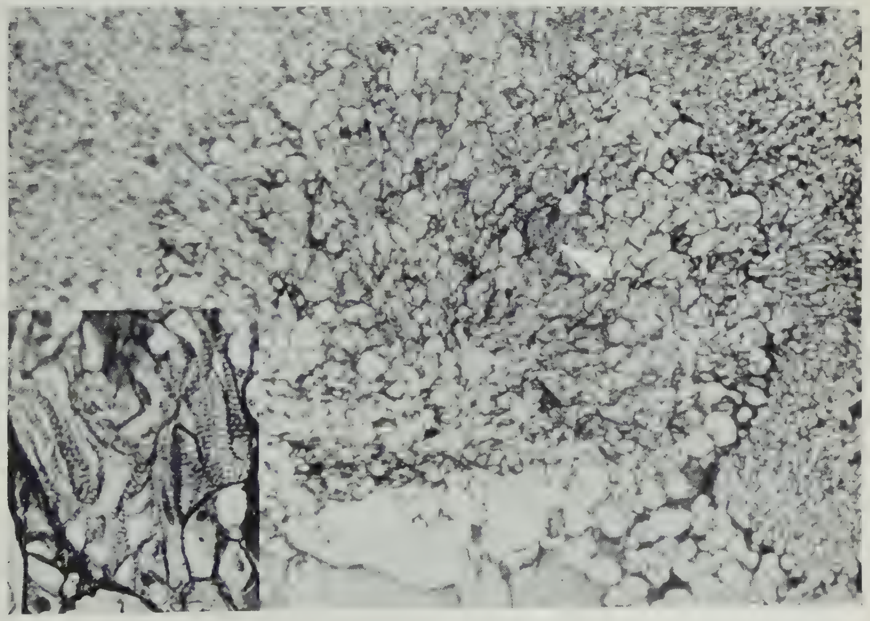

Plate 5b. *Sambucus nigra* var. *pendula*. New orientation in original explantate after 117 days cultivation. A group of lignified cells indicated by the arrow is reproduced much enlarged. 20 × resp. 120 ×.

Miss E. van Wijnen (now Mrs E. van Die née van Wijnen) has kindly made the photographs.

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A PLANT-GEOGRAPHICAL ANALYSIS OF THE LESSER SUNDA ISLANDS

BY

C. KALKMAN
(Rijksherbarium, Leiden)

(received March 27th, 1955)

I. INTRODUCTION

Many attempts have been made to divide the Malaysian area into two biogeographical parts, a western part of Asiatic affinity and an eastern part of Australian affinity. In order to define these parts more precisely a number of dividing lines (demarcations) have been proposed, which have only the central part (Makassar Straits) in common, but which south and north of that part deviate in two or more directions and which cross the Lesser Sunda Islands in different places. (For a review of these "lines", cf. Van Steenis 1948c and 1950b). They have been added to the "eastern part of Malaysia" (Wallace), to a central part "Wallacea" (Merrill) and together with Java to a separate province "South Malaysia" (Zollinger, Miquel, Van Steenis).

In the present analysis the composition and affinity of the Lesser Sunda Islands flora are studied, but it is not possible for me to give a judgment about the plant-geographical status of these islands within the Malaysian area. I leave this for those who have a more profound and all-round knowledge of the Malaysian flora.

The flora of the Lesser Sunda Islands is comparatively reasonably well known. Unfortunately most collections have only been identified provisionally and few of these lists have been published. As a result it is impossible to derive from literature a complete survey of the flora as to its species. Moreover, for our plant-geographical aims such a list should be as critical as possible. For these reasons I have refrained from framing a new enumeration.

The principal collections which have been listed are those of:

Leschenault, Riedlé etc., 1801, 1803 and other early French expeditions	Decaisne (1834)
Spanoghe, 1831–1836	Spanoghe (1835, 1841)
Zollinger, 1846–1847, 1857.	Zollinger (1845), Zollinger (1854–55), Zollinger (1857), Choisy (1858)

Forbes, 1882–1883	Forbes (1885), Baker, Rendle, Moore c.s. (1924–1926)
Naumann, 1875	Boeckeler (1884, Cyp.), Hackel (1885, Gram.), Kraenzlin (1886, Orchid.), Engler (1886)
Elbert, 1909–1910	Hallier (1912, 1914, 1918), J. J. Smith (1925, Orchid.), Koster (1933, Compos.)
Rensch, 1927	Von Malm (1934, partly)
Stein, 1932	Von Malm (1937, partly)
De Voogd, 1933–1936	De Voogd (1936–1941)
Mountain plants, various collectors	Van Steenis (1936b)
Bloembergen, 1939	Bloembergen (1940)
C. du Bois, 1939 (useful plants)	Van Steenis (1948a)
Meijer Drees, 1946–1947	Meijer Drees (1951)
Collections of trees in Forest Research Institute Bogor	Hildebrand (1953)

The genera and species mentioned in these publications, in revisions and monographs, and in the Flora Malesiana, as recorded from the Lesser Sunda Islands, have been compiled in a card system with annotations on their general geographic distribution.

Concerning the species (chapter III) a distinction was made between those which have been revised recently and which have not. Only the first group has been taken into consideration for the analysis.

Concerning the genera (chapter II) data have been obtained mostly from MS lists compiled by Dr Van Steenis, under whose supervision this survey was made [1] in order to verify the results to which he had come formerly (1936b) when basing his conclusions on the distribution of microthermic genera and their species in the Lesser Sunda Islands (78 species). These conclusions were, leaving out those which bear only on mountain plants:

1. There is no difference in distribution between the volcanic and non-volcanic islands (Sumba, Timor).
2. The Lesser Sunda Islands possess relatively few endemic species.
3. There is very close relationship with the flora of Java.
4. In relation to Java the Lesser Sunda Islands are rather poor in mountain plants.
5. This depauperization of Javan elements is not coincident with an increase of eastern elements, which emphasizes the abrupt demarcation of Timor against Australia, New Guinea, and the Moluccas.

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[1] His recent collection made in Timor (1953–1954) has not been taken into consideration.

6. The eastern element is certainly present but is not more pronounced than it is in Java.

7. The southern extremity of WALLACE's line between Bali and Lombok has no importance.

II. DISTRIBUTION OF THE GENERA

a. TYPES OF DISTRIBUTION

The distribution has been traced for the genera which are known to me to occur in the Lesser Sunda Islands. They have been arranged according to 5 types of distribution in Table I. Some 110 genera, which should not enter a plant-geographical discussion viz.: genera only represented by cultivated plants, plants escaped from cultivation, aliens and weeds, have been omitted. In the 4th column the figures for the whole of Malaysia are cited for comparison (figures taken from VAN STEENIS, 1950b).

TABLE I [1]

	Lesser Sunda Islands		Malaysia %
	number	%	
Type 1 – Genera occurring in continental Asia, Malaysia and Australia, without showing a special centre of development in this area	439	58.8	27.7
Type 2 – Centre of distribution in Asia; not or hardly occurring in Australia	176	23.5	26.3
Type 3 – Centre of distribution in Malaysia, eventually with some outposts in continental Asia or Australia	109	14.6	26.6
Type 3A – Local-endemic genera, from one island or group of islands (i.c. the Lesser Sunda Islands) only	2	0.3	13.8
Type 4 – Centre of distribution in Australia and/or the Pacific or Subantarctic regions, not or scarcely represented in Asia (types 4 and 5 of VAN STEENIS (1950b) combined)	21	2.8	5.7
	747	100.0	100.1

[1] The complete list of genera is to be found in Appendix I.

b. CONCLUSIONS AND REMARKS ON SOME TYPES

1. The Lesser Sunda Islands possess very many genera with a wide distribution (type 1), the percentage of those being more than twice as high as that for Malaysia as a whole. This "ground-tissue" of the Malaysian flora is apparently more predominant in the Lesser Sunda Islands than it is in the other parts of Malaysia.

2. The western-centred genera (type 2) form the group second-best represented in the Lesser Sunda Islands. The percentage of this group corresponds with the average for the whole of Malaysia.

3. The Lesser Sunda Islands are relatively very poor in autochthonous Malaysian elements (type 3). This group comprises also genera with a restricted area, the "sub-endemics":

Lamiacanthus O.K. (Acanth.), two species: *L. renschiae* Brem. in Lombok and *L. viscosus* O.K. in Central and East Java.
Muellerargia Cogn. (Cuc.), one species: *M. timorensis* Cogn. in Madura, Thursday Isl. and Timor.
Sclerachne R. Br. (Gram.). one species: *S. punctata* R. Br. in Java (the whole), Kangean, Bali, Sumba and Timor.
Teyleria Back. (Leg.), one species: *T. koordersii* (Back.) Back. in the whole of Java and in Flores.

4. The group of endemic genera (type 3A) is very small. In the Flora Malesiana VAN STEENIS (1950b, p. lxxi, fig. 20) mentions four genera, endemic in the Lesser Sunda Islands. These four genera were:

Aconceveibum Miq. (Euph.)	*Sautiera* Decne (Acanth.)
Paracelsea Zoll. 1857 (Euph.)	*Schizopremna* Baill. (Verb.)

Only one of these can now be retained viz. *Sautiera*. *Aconceveibum* and *Paracelsea* have been reduced to genera of type 1, viz. to *Mallotus* and *Acalypha* respectively, according to MERRILL & VAN STEENIS (1952). *Schizopremna* is a very dubious case. It is only known from the type and LAM & BAKHUIZEN VAN DEN BRINK (1921) doubt whether it is a separate genus and even whether it is indeed a Verbenacea; neither they, nor MOLDENKE (in litt.) have been able to examine the type.

The two endemic genera recognized here are:

Sautiera Decne (Acanth.), one species: *S. tinctorum* Decne in Timor, and
Xanthostachya Brem. (Acanth.), segregated from *Strobilanthes*. The genus has according to BREMEKAMP (1944) two species: *X. aspera* (Decne) Brem. in Timor and *X. arborea* (Span.) Brem. in Roti.

5. The percentage of eastern-centred genera is very small, even much smaller as compared with the average for the whole of Malaysia. The following genera belong to this group:

Alectryon Gaertn. (Sapind.). Centre of distribution in Australia and the Pacific, extending not further westward than the Philippines, Celebes, Kangean and East-Java. One or two species occur in the Lesser Sunda Islands.
Atalaya Bl. (Sapind.). Save *A. salicifolia* (DC.) Bl., which occurs also in Sumbawa, Sumba and Timor, this genus is wholly Australian.
Caladenia R. Br. (Orchid.). Australian genus, one species (*C. carnea* R. Br.) occurs in Australia, Tasmania, N. Zealand and N. Caledonia and in Malyaisa, viz. in Central and East Java, Bali, Lombok, S. Celebes and N. Guinea. (*C. javanica* Benn. ex Ridl. is mentioned by FORBES, 1885, for Timor!).
Casuarina L. (Cas.). When the widely-distributed coastal plant *C. equisetifolia* L. is left out of consideration, the genus is Australian, save some 5 or 6 species in Malaysia. *C. junghuhniana* Miq. occurs in E. Java, Bali, Sumba and Wetar.
Delarbrea VIEILL. (Aral.). Known from Australia and N. Caledonia, and N. Guinea; one species (*D. collina* Vieill.) in Timor and the Tenimber Islands.
Diuris Sm. (Orch.). Exclusively Australian, in Timor one species (*D. fryana* Ridl.).
Eucalyptus l'Hér. (Myrt.). Centre of distribution (500–700 species) in Australia, reaching westwards to Central Flores, Celebes, and the Philippines. In N. Guinea about 6 species. In the Lesser Sunda Islands the widely distributed *E. alba* Reinw. and one or two endemic species.

Exocarpus Labill. (Santal.). Centre in the Australian-Pacific region, *E. latifolius* R. Br. extending westwards to the Philippines, Celebes, and E. Java, apparently also in Indo-China; *E. pullei* Pilg. in Sumbawa and New Guinea.

Geitonoplesium A. Cunn. (Liliac.). Distributed in Australia, W. Pacific area and in Malaysia in N. Guinea, Moluccas, Lesser Sunda Islands, and possibly in E. Java according to Schlittler (1951).

Gomphrena L. (Amaranth.) has its centre in tropical America, and a few species in Australia and S. E. Malaysia. *G. canescens* (Poir.) R. Br. in N. Australia, the Tenimber Islands, and Timor, *G. tenella* (Moq.) Benth. in N. Australia and in Flores or the Moluccas (See Backer, 1949). Although this genus has its centre not in Australia, it is with respect to the Malaysian flora a distinctly eastern element.

Josephinia Vent. (Pedal.). The only species, *J. imperatricis* Vent., in N. and N.E. Australia, N. Guinea, Celebes, the Lesser Sunda Islands (Bali, Lombok, Sumbawa, Sumba, Timor) and E. Java (See Backer, 1951). Recently an African species has been referred to this genus (Bruce, 1953).

Microtis R. Br. (Orch.). Centering in Australia, one species in N. Caledonia, one species also in Malaysia, westward to the Philippines, Celebes and Java. The Australian species *M. parviflora* R. Br. is mentioned in Forbes (1885) for Timor.

Osbornia F. v. M. (Myrt.). The only species, *O. octodonta* F. v. M., in Australia, N. Guinea, Lesser Sunda Islands (Bali, Sumbawa, Timor), Celebes, Philippines, and N. Borneo (See Van Steenis, 1936a).

Pimelea B. & S. ex Gaertn. (Thymel.). Mainly Australian, some species in N. Guinea, 1 or 2 species in the Lesser Sunda Islands (Sumba, Timor) and one species in the Philippines.

Polyscias Forst. (Aral.). In Australia and N. Caledonia, in Malaysia in N. Guinea, Timor, Moluccas, and the Philippines.

Ptilotus R. Br. (Amaranth.). Nearly restricted to Australia, one species (*P. conicus* R. Br.) in N. Australia, S. Moluccas (Tenimber and Key Islands) and Lesser Sunda Islands (Sumba, Flores, Wetar, Roti, Timor). (See Backer, 1949).

Santalum L. (Santal.). All members of the genus in the Australian-Pacific region, except *S. album*, which occurs (in a wild state) only in Central Celebes, Sumba, Sawu, Timor and perhaps E. Java, and its nearest ally *S. papuanum* Summerh. from South New Guinea.

Stylidium Sw. ex Willd. (Styl.). The majority of the species in Australia, some extending to the Asiatic continent. In Sumba and W. Java: *S. javanicum* Sloot. (See Van Slooten, 1954).

Styphelia R. Br. (Epacr.). Centering in Australia, also some in the Pacific region, some species in N. Guinea, one species extending to Cochinchina, few species (perhaps 5–10) in the rest of Malaysia.

Thelymitra Forst. (Orch.). Centre of development in Australia, further in Tasmania, N. Zealand and N. Caledonia, one species in N. Guinea and one species (*T. javanica* Bl.) in the Philippines, Lombok, and Java. (*T. forbesii* Ridl. is mentioned in Forbes (1885) for Timor.)

Trachymene Rudge (Umb.). Mainly Australian and in N. Caledonia and Fiji, in Malaysia in New Guinea, Lesser Sunda Islands, Celebes, Philippines and Borneo. *T. acerifolia* Norm. in Celebes, Flores and Timor (See Buwalda, 1949).

In Table II the distribution has been given of the genera of type 4, from this table it is seen that:

a) out of 21 genera only 2 (*Atalaya*, *Diuris*) are in Malaysia restricted to the Lesser Sunda Islands; two more genera (*Gomphrena*, *Ptilotus*) occur in Malaysia besides in the Lesser Sunda Islands only in the South Moluccas (Tenimber- and Key Islands);

b) of the 21 genera 8 (or at most 10) are not found further westwards than the line west of the Philippines, Celebes, Lesser Sunda Islands;

c) of the 21 genera 9 (or at most 11) also occur in Java (see further next paragraph).

TABLE II

Distribution of some Eastern genera in Malaysia [1]

	MP	S	B	Ja	Ph	C	LSI	Mol	NG
Alectryon				×	×	×	×	×	×
Atalaya							×		
Caladenia				×		×	×		×
Casuarina	×	×	×	×	×	×	×	×	×
Delarbrea							×	×	×
Diuris							×		
Eucalyptus					×	×	×	×	×
Exocarpus				×	×	×	×	×	×
Geitonoplesium				?			×	×	×
Gomphrena							×	×	
Josephinia				×		×	×		×
Microtis				×	×	×	×		
Osbornia			×		×	×	×		×
Pimelea					×		×		×
Polyscias					×		×	×	×
Ptilotus							×	×	
Santalum				?		×	×		×
Stylidium	×	×		×	×	×	×	×	×
Styphelia	×	×	×	×	×	×	×	×	×
Thelymitra				×	×		×		×
Trachymene			×		×	×	×		×
Total	3	3	4	9(11)	12	12	21	11	16

[1] The abbreviations in the columns mean: MP = Malay Peninsula, S = Sumatra, B = Borneo, Ja = Java, Ph = Philippines, C = Celebes, LSI = Lesser Sunda Islands, Mol = Moluccas, NG = New Guinea.

6. Relationship with Java. As is said above, about half of the eastern-centred genera are also represented in Java. It appears further that the 4 genera with a restricted area (see p. 203) are practically confined to the Lesser Sunda Islands and Java (and/or its neighbouring islets). Thirdly, the close relationship of the floras of Java and the Lesser Sunda Islands is stressed by the fact that there are several genera which are distributed all over Malaysia, but appear absent from Java and the Lesser Sunda Islands. An examination of partly unpublished maps of VAN STEENIS gave the following list of 16 genera, which are represented in *all* islands or groups of islands of Malaysia, except in Java and the Lesser Sunda Islands.

Agathis (Conif.)
Bromheadia (Orch.)
Campnosperma (Anac.)
Endospermum (Euph.)
Firmiana (Sterc.)
Gymnacranthera (Myrist.)
Kayea (Gutt.)
Lucinaea (Rub.)
Matthaea (Mon.)
Oreobolus (Cyp.)
Pentaphragma (Camp.)
Petraeovitex (Vit.)
Santiria (Burs.)
Serianthes (Leg.)
Teysmanniodendron (Verb.)
Xylopia (Annon.)

A similar set of 15 genera is not represented in Java and the Lesser Sunda Islands, but for the rest occurs in *all but one* of the islands or island-groups in Malaysia:

Baeckea (Myrt.)
Brackenridgea (Ochn.)
Claderia (Orch.)
Cyrtostachys (Palm.)
Deplanchea (Bign.)
Dictyoneura (Sapind.)
Ixonanthes (Lin.)
Kurrimia (Celastr.)
Lepironia (Cyp.)
Osmelia (Flac.)
Pentaspadon (Anac.)
Plagiostachys (Zing.)
Pternandra (Melast.)
Rhodomyrtus (Myrt.)
Schoenus (Cyp.)

For still other genera which occur on both sides of the Line of Wallace, but fail to turn up in Java and the Lesser Sunda Islands, cf. Van Steenis (1932).

c. Summary of the conclusions, drawn from the distribution of the genera

The flora of the Lesser Sunda Islands, as regards the genera, for the greater part consists of widely distributed Old World elements. The Asiatic elements are normally extant, but notwithstanding the short distance to the Australian continent, there is no substantial admixture of eastern elements. Autochthonous Malaysian elements are rather poorly represented. Only two endemic genera are recognized, one of which is a segregate from a larger genus and the other is not recently revised. Finally there is a remarkable parallel with the flora of Java, both in presence of some elements peculiar to South-Malaysia, and in the absence of a number of genera from both areas.

III. THE DISTRIBUTION OF THE SPECIES

a. Types of distribution

It is clear that phytogeographical analyses should be based as much as possible on taxa which have been thoroughly revised. Therefore, I have refrained from trying to trace the distribution of all species which have been recorded from the Lesser Sunda Islands and have limited my work to revisions of Malaysian taxa posterior to 1925.

The main sources of reliable information have been:

"Contributions à l'étude de la flore des Indes néerlandaises" (Bull. Jard. Bot. Buitenzorg);

"Flora Malesiana" series I, vol. 4;

revisions and monographs in "Blumea", "Bull. Jard. Bot. Buitenzorg", "Reinwardtia", etc.;

some MS to be published in "Flora Malesiana";

some monographs in the "Pflanzenreich".

Use has further been made of lists (results of expeditions, publications of the Forest Research Institute, Bogor), sometimes checked with the material preserved in the Rijksherbarium, Leiden.

The records thus selected, may be regarded as reliable (see for the discussion p. 210).

The species have been arranged in five types of distribution, viz.:

type 1 – distributed in Continental Asia, Malaysia and Australia;
type 2 – distributed in Continental Asia and Malaysia, absent from Australia;

type 3 – not known outside the Malaysian area;
type 3A – endemic in the Lesser Sunda Islands;
type 4 – distributed in Malaysia and Australia, absent from Continental Asia.

In Appendix II an account has been given of 480 species, belonging to 210 genera and 51 families, which occur in this selected list. The results of the analysis have been compiled in Table III.

TABLE III

Type	Bali		Lombok		Sumbawa		Sumba		Flores		Alor		Wetar		Timor		Lesser Sunda Islands	
		%		%		%		%		%		%		%		%		%
1	61	35.3	42	33.6	43	34.7	58	47.9	33	35.9	5	38.5	32	50.8	119	42.3	155	32.3
2	55	31.8	32	25.6	35	28.2	29	24.0	20	21.7	2	15.4	14	22.2	57	20.3	125	26.0
3	43	24.9	31	24.8	31	25.0	20	16.5	27	29.3	4	30.8	9	14.3	48	17.1	110	22.9
3A	9	5.2	13	10.4	6	4.8	6	5.0	3	3.3	–	–	4	6.3	29	10.3	59	12.3
4	5	2.9	7	5.6	9	7.3	8	6.6	9	9.8	2	15.4	4	6.3	28	10.0	31	6.5
total	173		125		124		121		92		13		63		281		480	

b. Conclusions and additional remarks on some types

1. About one third of the species has a wide distribution in the Old World tropics. (type 1).
2. About one fourth belongs to species which are restricted to Malaysia (type 3).
3. Only 12 % of the species are endemic in the Lesser Sunda Islands. Among the species considered there are 59 endemic species, 8 of which are known from more than one island.

These 59 species belong to 31 genera: 18 of those genera belong to the distributional type 1, 4 genera to type 2, 7 to type 3, 1 to type 3A and 1 to type 4.

Lombok and Timor have the highest percentage of endemics, the other islands are about mutually equal in this respect.

Table IV contains a survey of the surface of each island in sq. km, the highest peak in metres, and the percentage of endemic species. It is remarkable that Lombok and Timor, with their highest percentage of endemics have either the highest peak or the largest surface.

TABLE IV

	% endem.	sq. km	highest peak
Bali	5.2	5770	3124
Lombok	*10.4*	4715	*3726*
Sumbawa.	4.8	15450	2851
Sumba	5.0	11150	1225
Flores	3.3	15000	3282
Alor	—	2885	1765
Wetar	6.3	3500	1412
Timor	*10.3*	*28090*	2920

4. 31 species are represented in our list, of which the distribution is limited to Australia and/or the Pacific and Malaysia. These 31 species belong to 31 genera and these genera are distributed over the types as follows: 25 genera of *type 1*; 3 of *type 3*; 3 of *type 4*.

Of the 31 species only 3 appear to be typically Australian-distributed, the others are apparently mostly eastern representatives of widely dispersed genera.

5. The percentage of western elements (type 2) is – for the whole of the Lesser Sunda Islands – about four times as large as that of the eastern elements (type 4). In Fig. 1 the percentages of eastern and western species have been represented, that is respectively of types 4 and 2.

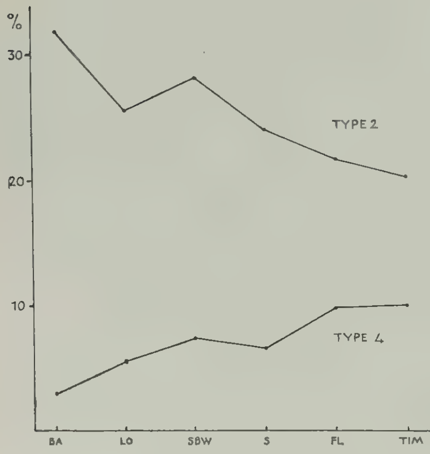

Fig. 1.

Percentages of species type 2 (western-distributed) and type 4 (eastern-distributed) for each island.

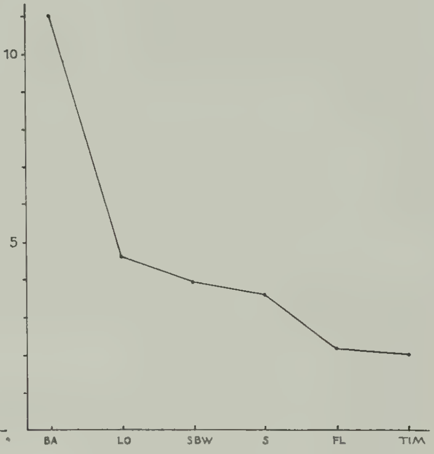

Fig. 2.

Ratio number of western species (type 2) to number of eastern species (type 4) for each island.

BA = Bali, LO = Lombok, SBW = Sumbawa, S = Sumba, FL = Flores, TIM = Timor.

From this Fig. the following conclusion can be drawn:

a) In each island Western elements form the majority;
b) the percentage of Western elements decreases from West to East;
c) the percentage of Eastern species decreases from East to West.

The decreases mentioned under *b*) and *c*) are not very strong, but still significant.

Fig. 2 shows the ratio of Western to Eastern species (i.e. type 2: type 4) for each island separately. This ratio gradually decreases towards the East; only between Bali and Lombok there is a slight demarcation, the ratio in Bali being 11.0, in Lombok 4.6. This is the only indication in favour of the southern extremity of Wallace's Line between these islands.

6. Difference between volcanic and non-volcanic islands. A survey of the species listed in Appendix II shows that:

ca 33 % of the species occur (in the Lesser Sunda Islands) *only* in one or more of the islands of the upper row, which are volcanic (Bali, Lombok, Sumbawa, Flores, Alor, Wetar);
ca 24 % occur *only* in the non-volcanic islands Sumba and/or Timor;
ca 43 % of the species are found in islands of the upper row *as well as* in islands of the lower row.

I do not believe that these figures can be interpreted as an indication of existing difference between the floras of volcanic and non-volcanic islands, the more so because the majority of the 24 % are known only from Timor, the largest and best-explored island of all.

c. SUMMARY OF THE CONCLUSIONS, DRAWN FROM THE DISTRIBUTION OF THE SPECIES

The flora of the Lesser Sunda Islands consists for the greater part of species which are widely distributed in the Old World tropics. About 1/4 of the species belongs to the autochthonous Malaysian element. Western species are in the majority in all islands of the series; their percentage decreases eastwards, whereas the percentage of eastern species decreases in the reverse direction. There is only one demarcation in the series, viz. between Bali and Lombok, but its importance is faint. Only 12 % of the species are endemic for the Lesser Sunda Islands; the highest numbers of endemics are found in Lombok and Timor. Both islands are topographically outstanding in the series, Lombok having the highest peak, Timor possessing the largest surface. There is no appreciable difference in botanical composition between the volcanic and the non-volcanic islands.

IV. RELIABILITY OF THE DATA

a. GENERA

The figures of Table I are of course not final. It is to be expected that there will be future changes due to the increase of knowledge of the Malaysian flora. Our present insight into the taxonomical composition of the Malaysian flora is, however, already so much advanced that these future changes and additions will not attack the essential features of the picture.

The list of Australian-Pacific genera (p. 203) is rather complete and probably accurate in outline. This does not hold for Table II in which changes can be expected.[1]

The lists of genera which are hitherto unknown from Java and the Lesser Sunda Islands, have been drawn only to give an idea of their existence; these lists are not intended to be complete.

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[1] After the manuscript of this paper was completed, a specimen of *Exocarpus latifolius* from N. Borneo was found among new acquisitions of the Rijksherbarium.

b. Species

The list of species in Appendix II has been compiled as accurately as possible from literature. In cases where this source was incomplete, the collections of the Rijksherbarium have been consulted for additional information. These collections are unfortunately much less rich in specimens from different localities as compared with the Herbarium Bogoriense where such a study could be made with better advantage. This unavoidable situation and the fact that even the best monograph is not complete at the date of its publication, are the reasons why these data cannot be considered to be final.

Even though, I estimate the figures of the percentages in Table III to have a rather high value because of two arguments, viz.

a) Data have been obtained at random. They comprise 480 species from very different families and genera which have been revised since 1925 without preference for special greater divisions of the Phanerogams. From Table V can be concluded that these 480 species, estimated at about 10 % of the total flora, are representative for it. In this table a comparison has been made between the genera of which species have been considered and the total number of genera known from these islands.

TABLE V

	Genera of which the species are listed in appendix II		Percentage of all genera of the Lesser Sunda Islands (compare Table I)
Type		%	%
1	133	63.3	58.8
2	40	19.0	23.5
3	30	14.3	14.6
3A	1	0.5	0.3
4	6	2.9	2.8
Total	210	100.0	100.0

From this Table it appears that the figures in the third and fourth columns are in excellent agreement, which shows that the species taken into consideration give a tolerable picture (cross section) of the whole flora.

b) The exploration of the different islands is approximately of the same degree. The figures on the last line of Table III are of approximately the same order, Alor and Wetar excepted; Flores and Timor deviate slightly. For Flores the figure is too low, which I assume to be due to less intensive exploration. The figure for Timor is high, because of a relative intense exploration and publication, and besides, possibly, because the island is richer partly on account of its greater size. Even though, the *percentages* for Timor fit well into the picture.

In conclusion I assume that, although the figures are not final in detail and liable to future change, they are comparable and will compute roughly with the real plant-geographic composition.

c. COMPARISON OF RESULTS BY USING GENERA AND SPECIES

In a chorological study the chosen unit may be the genus (including subgenera or sections) or it may be the species.

In both cases the difficulty is that the entities are not wholly comparable. For instance the three genera, *Cycas*, *Ficus* and *Xanthostachya* are not comparable. The same holds for the species.

To cope with this discordance, it is necessary that chorological considerations should be based on a large statistic of entities from many different groups. The numbers used in this study (747 genera and 480 species) I believe to be sufficient for this aim.

It is to be expected that there will be a different outcome if genera are used as the unit instead of the species. A priori it is probable that, whatever the area considered may be, the number of restricted areas of distribution is larger in the species than in the genera, and conversely the number of large areas of distribution is smaller in the species than among the genera. This is true for the Lesser Sunda Islands and has been illustrated in Table VI.

TABLE VI

		Genera in % (Table I)		Species in % (Table III)	
Type 1	Large areas. . . .		58.8		32.3
Type 2	Medium-sized areas	23.5	26.3	26.0	32.5
Type 4		2.8		6.5	
Type 3	Small areas. . . .	14.6	14.9	22.9	35.2
Type 3A		0.3		12.3	

It appears that, notwithstanding the differences to be expected by taking either the genus or the species as the unit for the considerations, the general chorological features emerging from the analysis are very similar in both cases.

SUMMARY

It has appeared, and it is in itself remarkable, that the conclusions drawn by VAN STEENIS (1936b) from an analysis of the microtherm genera in the Lesser Sunda Islands (see p. 201) are confirmed by the present very much larger survey of the flora.

According to Malaysian standards the Lesser Sunda Islands flora is a relatively poor one, of predominantly Asiatic affinity, most closely allied to that of Java, rich in species and genera with wide areas, poor in autochthonous elements (endemics and subendemics), and without any important supplementary Eastern elements which might be expected on the basis of its geographical situation close to the Australian continent.

Within the Lesser Sunda Islands the percentage of Western-distributed elements decreases from Bali eastward to Timor, whereas the number of Eastern elements decreases in the reverse direction.

The figure indicating the ratio of the percentages Western to Eastern elements per island decreases markedly from Bali to Lombok but then gradually eastward, which gives a faint indication of a demarcation between Bali and Lombok.

There is no significant difference in botanical composition between volcanic and non-volcanic islands.

It has appeared that by taking either the genus or the species as the unit for the considerations, the general picture emerging from the analysis is similar in both cases.

APPENDIX I.

Types of distribution of the genera

Type 1 — *Acanth.*: Acanthus, Dicliptera, Hemigraphis, Hypoestes, Justicia, Ruellia (incl. Dipteracanthus). — *Aizoac.*: Glinus, Sesuvium, Trianthema. — *Amaranth.*: Alternanthera, Cyathula, Deeringia. — *Amaryll.*: Crinum, Curculigo, Hypoxis. — *Anacard.*: Buchanania, Rhus. — *Anon.*: Saccopetalum, Uvaria. — *Apoc.*: Alstonia, Alyxia, Cerbera, Ervatamia, Ochrosia, Parsonsia, Wrightia. — *Arac.*: Amorphophallus, Typhonium. — *Arist.*: Aristolochia. — *Ascl.*: Ceropegia, Cynanchum, Gymnanthera, Gymnema, Marsdenia, Secamone, Tylophora. — *Bign.*: Dolichandrone. — *Bomb.*: Gossampinus. — *Bor.*: Cordia, Cynoglossum, Ehretia, Tournefortia, Trichodesma. — *Burs.*: Canarium, Garuga, Protium. — *Camp.*: Lobelia, Pratia, Wahlenbergia. — *Capp.*: Cadaba, Capparis. — *Capr.*: Sambucus. — *Caryoph.*: Polycarpon, Stellaria. — *Cel.*: Celastrus, Elaeodendron, Euonymus. — *Chen.*: Arthrocnemon, Salsola. — *Combr.*: Lumnitzera, Terminalia. — *Comm.*: Aneilema, Commelina, Cyanotis, Pollia. — *Comp.*: Adenostemma, Blumea, Centipeda, Conyza, Ethulia, Gnaphalium, Gynura, Pluchea, Pterocaulon, Senecio, Vernonia, Wedelia. — *Conif.*: Dacrydium. — *Conn.*: Connarus. — *Conv.*: Argyreia, Cuscuta, Erycibe, Evolvulus, Ipomoea, Jacquemontia, Merremia, Operculina, Porana, Stictocardia. — *Corn.*: Alangium. — *Cuc.*: Alsomitra, Melothria, Neoalsomitra, Trichosanthes. — *Cunon.*: Weinmannia. — *Cyc.*: Cycas. — *Cyp.*: Carex, Cyperus, Fimbristylis, Fuirena, Heleocharis, Remirea, Scirpus, Scleria. — *Dill.*: Dillenia, Tetracera. — *Diosc.*: Dioscorea. — *Dros.*: Aldrovanda, Drosera. — *Eben.*: Diospyros. — *Elaeagn.*: Elaeagnus. — *Elaeoc.*: Elaeocarpus, Sloanea. — *Elat.*: Bergia. — *Eric.*: Gaultheria. — *Euph.*: Acalypha, Andrachne, Antidesma, Bischoffia, Breynia, Bridelia, Claoxylon, Cleistanthus, Croton, Drypetes, Euphorbia, Excoecaria, Glochidion, Mallotus, Phyllanthus. — *Flac.*: Casearia, Homalium, Xylosma. — *Flag.*: Flagellaria. — *Gent.*: Limnanthemum. — *Geran.*: Geranium. — *Good.*: Goodenia, Scaevola. — *Gram.*: Apluda, Aristida, Arthraxon, Arundinella, Bambusa, Bothriochloa, Brachiaria, Brachyachne, Capillipedium, Centotheca, Chloris, Chrysopogon, Coelorhachis, Cymbopogon, Cynodon, Cyrtococcum, Deyeuxia, Dichantium, Digitaria, Dimeria, Echinochloa, Elythrophorus, Eragrostis, Eriochloa, Eulalia, Festuca, Hackelochloa, Heteropogon, Hyparrhenia, Isachne, Ischaemum, Iseilema, Leptaspis, Leptochloa, Lepturus, Ophiuros, Oplismenus, Panicum, Paspalidium, Paspalum, Perotis, Phragmites, Pogonatherum, Pseudechinolaena, Pseudopogonatherum, Rottboellia, Schizachyrium, Sehima, Setaria, Sorghum, Spinifex, Sporobolus, Thaumastochloa, Themeda, Tripogon, Zoisia. — *Gutt.*: Calophyllum, Garcinia, Hypericum. — *Hern.*: Gyrocarpus, Hernandia. — *Hipp.*: Hippocratea, Salacia. — *Hydr.*: Halophila, Ottelia. — *Lab.*: Anisomeles, Coleus, Moschosma, Orthosiphon, Plectranthus, Scutellaria, Teucrium. — *Laur.*: Beilschmiedia, Cassytha, Cinnamomum, Cryptocarya, Litsea, Neolitsea. — *Lecyth.*: Barringtonia. — *Leg.*: Abrus, Acacia, Adenanthera, Aeschynomene, Albizzia, Alysicarpus, Bauhinia, Caesalpinia, Canavalia, Cantharospermum, Cassia, Crotalaria, Cynometra, Dalbergia, Derris, Desmodium, Dichrostachys, Eriosema, Erythrina, Flemingia, Galactia, Indigofera, Intsia, Lespedeza, Lourea, Mesoneurum, Millettia, Mucuna, Peltophorum, Phaseolus, Pithecellobium, Pongamia, Psoralea, Rhynchosia, Sesbania, Smithia, Sophora, Tephrosia, Uraria, Vigna, Zornia. — *Lil.*: Asparagus, Cordyline, Dianella, Pleomele, Smilax. — *Log.*: Cynoctonum, Fagraea, Geniostoma, Mitrasacme, Strychnos. — *Lor.*:

Dendrophtoe, Korthalsella, Viscum. — *Lythr.*: Ammannia, Lagerstroemia, Pemphis. — *Malv.*: Abelmoschus, Abutilon, Hibiscus, Sida, Thespesia. — *Melast.*: Osbeckia. — *Mel.*: Aglaia, Amoora, Dysoxylum, Melia, Toona, Turraea, Xylocarpus. — *Menisp.*: Cissampelos, Pachygone, Pycnarrhena, Stephania, Tinospora. — *Mor.*: Antiaris, Cudrania, Fatoua, Ficus, Malaisia. — *Myrs.*: Aegiceras, Ardisia, Embelia, Maesa, Rapanea. — *Myrt.*: Cleistocalyx, Decaspermum, Eugenia, Leptospermum, Melaleuca. — *Naj.*: Najas. — *Nyct.*: Boerhaavia, Pisonia. — *Olac.*: Ximenia. — *Oleac.*: Jasminum, Linociera, Olea. — *Onagr.*: Epilobium, Jussiaea. — *Opil.*: Cansjera. — *Orch.*: Bulbophyllum, Calanthe, Dendrobium, Eulophia, Goodyera, Habenaria, Liparis, Microstylis, Spiranthes. — *Oxal.*: Biophytum. — *Palm.*: Arenga, Borassus. — *Pand.*: Freycinetia, Pandanus. — *Pass.*: Adenia, Passiflora. — *Pip.*: Peperomia, Piper. — *Pitt.*: Pittosporum. — *Plumb.*: Aegialitis. — *Podoc.*: Podocarpus. — *Polygal.*: Polygala. — *Polygon.*: Polygonum, Rumex. — *Pont.*: Monochoria. — *Port.*: Portulaca. — *Prim.*: Lysimachia. — *Ranunc.*: Clematis, Ranunculus.— *Rhamn.*: Colubrina, Gouania, Zizyphus.— *Rhiz.*: Bruguiera, Carallia, Ceriops, Rhizophora. — *Ros.*: Parinarium, Pygeum, Rubus. — *Rub.*: Borreria, Dentella, Galium, Gardenia, Geophila, Guettarda, Knoxia, Morinda, Nauclea, Nertera, Oldenlandia, Pavetta, Plectronia, Randia, Spermacoce, Tricalysia, Wendlandia. — *Rut.*: Acronychia, Clausena, Evodia, Fagara, Glycosmis, Micromelum. — *Sapind.*: Allophylus, Arytera, Dodonaea, Erioglossum, Guioa, Harpullia, Mischocarpus, Pometia. — *Sapot.*: Manilkara, Mimusops, Palaquium. — *Sax.*: Polyosma. — *Scroph.*: Bacopa, Buechnera, Ilysanthes, Lindernia, Mazus, Sopubia, Striga. — *Simar.*: Brucea, Harrisonia. — *Sol.*: Solanum. — *Sonn.*: Sonneratia. — *Sterc.*: Helicteres, Heritiera, Kleinhovia, Melhania, Melochia, Pterospermum, Sterculia. — *Sympl.*: Symplocos. — *Tacc.*: Tacca. — *Thym.*: Wikstroemia. — *Til.*: Grewia, Triumfetta. — *Typh.*: Typha. — *Ulm.*: Celtis, Trema. — *Umb.*: Centella, Hydrocotyle, Oenanthe. — *Urt.*: Boehmeria, Elatostema, Fleurya, Laportea, Pouzolzia. — *Verb.*: Avicennia, Callicarpa, Clerodendrum, Gmelina, Phyla (Lippia), Premna, Vitex. — *Viol.*: Hybanthes. — *Vit.*: Cissus. — *Zing.*: Alpinia, Costus, Curcuma. — *Zyg.*: Tribulus.

Type 2 — *Acanth.*: Asystasia, Barleria, Blepharis, Isochoriste, Lepidagathis, Nomaphila, Peristrophe, Rungia, Seriocalyx, Ptyssiglottis, Thunbergia. — *Acer.*: Acer. — *Amaranth.*: Achyranthes, Aerva, Allmania, Pupalia. — *Anac.*: Dracontomelum, Mangifera, Spondias. — *Anon.*: Artabotrys, Mitrephora, Polyalthia. — *Apoc.*: Anodendron, Chonemorpha, Rauwolfia. — *Arac.*: Aglaonema, Arisaema, Remusatia. — *Aral.*: Schefflera. — *Ascl.*: Calotropis, Cryptolepis, Dischidia, Dregea, Telosma. — *Bals.*: Impatiens. — *Beg.*: Begonia. — *Bign.*: Millingtonia, Oroxylum, Radermachera. — *Buddl.*: Buddleia. — *Burm.*: Burmannia sect. Euburmannia.—*Capr.*: Lonicera, Viburnum. — *Chlor.*: Chloranthus. — *Clethr.*: Clethra. — *Combr.*: Combretum, Quisqualis. — *Comm.*: Forrestia. — *Comp.*: Anaphalis, Athroisma, Bidens, Dichrocephala, Emilia, Eupatorium, Inula, Lactuca, Laggera, Microglossa, Moonia, Myriactis. — *Conv.*: Hewittia. — *Crass.*: Kalanchoë. — *Cuc.*: Coccinia, Gynostemma, Momordica, Zanonia. — *Daphn.*: Daphniphyllum. — *Dat.*: Tetrameles. — *Dich.*: Dichapetalum. — *Eric.*: Rhododendron, Vaccinium. — *Euph.*: Alchornea, Cleidion, Gelonium, Homonoia, Putranjiva, Sauropus. — *Gent.*: Enicostemma, Exacum, Swertia. — *Gesn.*: Didymocarpus, Epithema, Rhynchothecum. — *Gnet.*: Gnetum. — *Gram.*: Brachypodium, Dendrocalamus, Garnotis, Gigantochloa, Microstegium, Miscanthus, Mnesithea, Muehlenbergia, Neyraudia, Saccharum, Schizostachyum, Streblochaete, Thelepogon. — *Gutt.*: Cratoxylon. — *Hern.*: Illigera. — *Jugl.*: Engelhardtia. — *Lab.*: Achyrospermum, Acrocephalus, Cymaria, Elsholtzia, Gomphostemma, Leucas, Mesona, Microtoena, Pogostemon, Satureia. — *Leg.*: Dolichos, Dumasia, Parochetus, Pseudarthria, Pterocarpus, Shuteria, Stylosanthes. — *Lil.*: Gloriosa. — *Lor.*: Scurrula. — *Lythr.*: Woodfordia. — *Magn.*: Manglietia, Michelia, Talauma. — *Malp.*: Hiptage. — *Mel.*: Cipadessa, Munronia. — *Menisp.*: Pericampylus. — *Myr.*: Myrica. — *Orch.*: Herminium, Phajus, Platanthera, Polystachya, Tropidia, Vanda, Zeuxine. — *Plumb.*: Plumbago. — *Ran.*: Thalictrum. — *Rhamn.*: Berchemia, Rhamnus. — *Ros.*: Photinia. — *Rub.*: Hymenodyction, Ixora, Mussaenda, Mycetia, Paederia, Psychotria, Tarenna. — *Rut.*: Atalantia, Boenninghausenia, Toddalia. — *Sal.*: Salix. — *Salv.*: Azima. — *Sapind.*: Lepisanthes, Sapindus, Schleichera. — *Sarc.*: Sarcosperma. — *Sax.*: Astilbe, Itea. — *Scroph.*: Torenia, Wightia. — *Simar.*: Picrasma. — *Sterc.*: Buettneria. — *Theac.*: Adinandra, Eurya. — *Ulm.*: Gironniera. — *Umb.*: Pimpinella, Sanicula. — *Urt.*: Debregeasia, Distemon, Girardinia, Oreocnide, Pilea. — *Viol.*: Rinorea. — *Vit.*: Leea, Vitis. — *Zing.*: Hedychium.

Type 3 — *Acanth.*: Lamiacanthus, Pararuellia. — *Anon.*: Anomianthus. — *Apoc.*: Vallaris, Voacanga. — *Arac.*: Epipremnum, Rhaphidophora. — *Aral.*: Arthrophyllum, Harmsiopanax. — *Ascl.*: Hoya. — *Bign.*: Pandorea. — *Bomb.*: Camptostemon. — *Corn.*: Mastixia. — *Cuc.*: Muellerargia. — *Dat.*: Octomeles. — *Eric.*: Diplycosia. — *Euph.*: Codiaeum, Homalanthus, Macaranga, Melanolepis, Pimeleodendron, Sumbavia, Trigonostemon. — *Flac.*: Pangium, Ryparosa. — *Gesn.*: Cyrtandra, Dichrotrichum, Rhynchoglossum, Trichosporum. — *Gram.*: Astenochloa, Polytrias, Sclerachne. — *Icac.*: Stemonurus (Gomphandra incl.). — *Laur.*: Actinodaphne. — *Lecyth.*: Planchonia. — *Leg.*: Phylacium, Teyleria. — *Lor.*: Amyema, Amylotheca, Dicymanthes, Ginalloa. — *Malp.*: Ryssopteris. — *Mar.*: Actoplanes. — *Melast.*: Astronia, Medinilla, Melastoma, Memecylon, Omphalopus, Otanthera, Sonerilla. — *Mel.*: Azadirachta, Chisocheton. — *Menisp.*: Anamirta. — *Mor.*: Artocarpus, Streblus, Taxotrophis. — *Myrist.*: Knema, Myristica. — *Opil.*: Champereia. — *Orch.*: Anoectochilus, Appendicula, Arundina, Ceratostylis, Coelogyne, Cordula, Dendrochilum, Dicerostylis, Didymoplexis, Eria, Macodes, Myrmechis, Nervilia, Oberonia, Peristylus, Pholidota, Pomatocalpa, Saccolabium, Sarcanthus, Schoenorchis, Spathoglottis, Taeniophyllum, Thrixspermum, Trichoglottis, Vrydagzynea. — *Palm.*: Corypha. — *Rub.*: Amaracarpus, Argostemma, Neonauclea, Ophiorrhiza, Timonius. — *Rut.*: Triphasia. — *Sapind.*: Elattostachys, Otophora, Tristiropsis. — *Sapot.*: Lucuma, Madhuca, Planchonella. — *Sol.*: Lycianthes. — *Sonn.*: Duabanga. — *Sterc.*: Pterocymbium. — *Thym.*: Phaleria. — *Til.*: Berrya, Schoutenia. — *Ulm.*: Parasponia. — *Urt.*: Cypholophus, Leucosyke, Procris. — *Vit.*: Ampelocissus. — *Zing.*: Globba.

Type 3A — *Acanth.*: Sautiera, Xanthostachya.

Type 4 — *Amaranth.*: Delarbrea, Gomphrena, Polyscias, Ptilotus. — *Cas.*: Casuarina. — *Epacr.*: Styphelia. — *Lil.*: Geitonoplesium. — *Myrt.*: Eucalyptus, Osbornia. — *Orch.*: Caladenia, Diuris, Microtis, Thelymitra. — *Pedal.*: Josephinia. — *Santal.*: Exocarpus, Santalum. — *Sapind.*: Alectryon, Atalaya. — *Thym.*: Pimelea. — *Umb.*: Trachymene. — *Urt.*: Pipturus.

APPENDIX II.

DISTRIBUTION OF THE SPECIES

The number in the second column indicates the type of distribution of the species (cf. p. 206), in the third column the islands are mentioned from which the species is known: B = Bali, L = Lombok, Sw = Sumbawa, S = Sumba, F = Flores, A = Alor (incl. Solor), W = Wetar, T = Timor (incl. Sawu, Roti, Kisar, Leti).

Acanthaceae:		
Dipteracanthus repens Hsk.	2	Sw
Hemigraphis decaisneana And.	3A	T
H. wetarensis Brem.	3A	W
Lamiacanthus renschiae Brem..	3A	L
Pararuellia napifera Brem.	3	Sw, F, W
Seriocalyx timorensis Brem.	3	B, Sw, T
Xanthostachya arborea Brem.	3A	T
X. aspera Brem.	3A	T
Aceraceae:		
Acer laurinum Hsk.	3	B, L, Sw, F, T
Aizoaceae:		
Glinus lotoides L.	1	B, S, T
G. oppositifolius DC.	1	Sw, T
Sesuvium portulacastrum L.	1	B, T

Trianthema portulacastrum L.	1	Sw, F, T
Tr. triquetra Willd.	1	B
Amaranthaceae:		
Achyranthes bidentata Bl.	1	B, L
Aerva lanata Juss.	1	T
A. sanguinolenta Bl.	2	L, Sw, F, T
Allmania nodiflora Wight	2	S, W
Alternanthera sessilis DC.	1	L, W, T
Deeringia amaranthoides Merr.	1	B, L, Sw, S, T
Gomphrena canescens R. Br.	4	T
Ptilotus conicus R. Br.	4	S, F, W, T
Pupalia lappacea Juss.	1	B, L, Sw, S, T
Bignoniaceae:		
Dolichandrone spathacea Sch.	1	W, T
Oroxylum indicum Vent.	2	T
Pandorea pandorana Steen.	4	L
Radermachera gigantea Miq.	3	B, F, T
Burmanniaceae:		
Burmannia coelestis Don	2	B
Burseraceae:		
Canarium asperum Bth.	3	Sw, S, F, T
C. commune L.	3	B, F, A, W, T
C. oleosum Engl.	3	A, T
Garuga floribunda Decne	1	B, L, Sw, S, F, W, T
Protium javanicum Burm.	3	B, L, Sw
Caprifoliaceae:		
Lonicera acuminata Wall.	2	B
L. javanica DC.	3	B
Sambucus javanica Bl.	2	B, L
Viburnum coriaceum Bl.	2	B, L, F, T
V. lutescens Bl.	2	B, L
V. sambucinum Bl.	2	Sw, F, T
Chenopodiaceae:		
Arthrocnemum indicum Moq.	1	Sw, S, T
Salsola kali L.	1	B, S, T
Combretaceae:		
Combretum latifolium Bl.	2	B, L, Sw, S, F
C. tetralophoides Sloot.	3A	F
C. trifoliatum Vent.	2	B
Lumnitzera littorea Voigt	1	F, T
L. racemosa Willd.	1	B, S, F, A, T
Quisqualis sulcata Sloot.	3	W
Terminalia bellirica Roxb.	2	B, W, T
T. catappa L.	1	B, Sw, F, W, T
T. citrina Flem.	2	T
T. copelandii Elm.	3	F
T. microcarpa Decne	3	L, T
T. soembawana Sloot.	3	Sw, T
T. zollingeri Exell	3A	Sw, T
Compositae:		
Adenostemma lavenia O.K.	1	B, F, T
A. macrophyllum DC.	2	L
A. parviflorum DC.	1	B, L, F
A. renschii Koster	3A	F
Ethulia megacephala Sch.–Bip.	1	B

E. triflora Koster	3A	T
Eupatorium nodiflorum Wall.	2	L
Vernonia albiflora Koster	3A	L
V. arborea Ham.	2	B, Sw, S
V. capituliflora Miq.	3A	Sw
V. cinerea Less.	1	B, L, S, W, T
V. coerulea Koster	3A	S, T
V. erigeroides DC.	4	L, Sw, F, T
V. floresiana Koster	3A	F
V. junghuhniana Koster	3	T
V. laxiflora Less.	3A	B, L, T
V. letiensis Koster	3A	T
V. moluccensis Miq.	3	B, L, T
V. patula Merr.	2	B, T
V. tengwallii Koster	3A	L
V. timorensis Koster	3A	T
V. walshae Koster	3A	T
V. wetarensis Koster	3A	W
Connaraceae:		
Connarus pentaphyllus Schell.	3A	T
Convolvulaceae:		
Argyreia bifrons Ooststr.	3A	L
A. glabra Choisy	3A	L
A. mollis Choisy	2	B
A. reinwardtiana Miq.	3A	T
A. sumbawana Ooststr.	3A	Sw
A. walshae Ooststr.	3A	T
Cuscuta timorensis Engelm.	3	W, T
Erycibe timorensis Hoogl.	3A	T
Evolvulus alsinoides L.	1	B, W, T
Hewittia sublobata O.K.	1	B, L, Sw, F, W, T
Ipomoea aculeata Bl.	2	L, Sw, A, W, T
I. aquatica Forsk.	1	Sw, T
I. asarifolia R. & S.	1	B
I. decaisnei Ooststr.	3	L, Sw, T
I. digitata L.	1	T
I. eriocarpa R. Br.	1	S, W, T
I. illustris Prain	2	B
I. maxima Sw.	1	L, S, F, T
I. nil Roth	1	L, Sw, S, T
I. obscura Ker-Gawl	1	L, Sw, S, W, T
I. ochroleuca Span.	3A	T
I. pes-caprae Sw.	1	B, L, Sw, T
I. pes-tigridis L.	1	B, L, S, F, T
I. plebeia R. Br.	4	L, Sw, T
I. polymorpha R. & S.	1	S, F, T
I. quamoclit L.	1	L, Sw, T
I. riparia Don	1	B
I. sumatrana Ooststr.	2	Sw, T
I. trichosperma Bl.	3	Sw, A, T
Jacquemontia paniculata Hall.	1	S, T
J. zollingeri Hall. f.	3	B, Sw, T
Merremia dichotoma Ooststr.	3A	T
M. emarginata Hall. f.	1	Sw, T
M. gemella Hall. f.	1	L, Sw
M. hederacea Hall. f.	1	T
M. tridentata Hall. f.	1	L, Sw, T
M. umbellata Hall. f.	1	F, W, T
M. vitifolia Hall. f.	2	F, T
Operculina riedeliana Ooststr.	2	F, W, T

O. turpethum Mauso	1	Sw, S, T
Porana racemosa Roxb.	2	B, L, Sw, T
P. volubilis Burm.	2	B, L, Sw, T
Stictocardia cordatosepala Ooststr.	3A	L
St. discolor Ooststr.	3A	T
St. neglecta Ooststr.	3	W, T
St. tiliifolia Hall. f.	1	L
Cornaceae:		
Alangium chinense Rehd.	2	B, Sw, S, F
A. rotundifolium Bloemb.	3	B
A. salvifolium Wang	2	B, Sw, S
A. villosum Wang	4	F, T
Mastixia rostrata Bl.	3	F
Crassulaceae:		
Kalanchoë integra O.K.	1	B, L, S, T
Cycadaceae:		
Cycas circinnalis L.	1	T
C. rumphii Miq.	4	Sw, S, F, A, T
Cyperaceae:		
Carex baccans Nees	2	B, L
C. brunnea Thb.	1	L, F
C. gembolensis Clarke	3	B, L, F, T
C. myosurus Nees	2	L
C. oblonga Nelm.	3	L
C. oligostachya Hook.	2	Sw, S, F
C. rafflesiana Boott	4	B, L, F, T
C. timorensis Nelm.	3A	T
Cyperus alopecuroides Rottb.	1	B, S
C. brevifolius Hsk.	1	L
C. bulbosus Vahl	1	T
C. compressus L.	1	F, T
C. cyperinus Valck.	1	L, Sw, W
C. cyperoides O.K.	1	S, T
C. difformis L.	1	B, T
C. elatus L.	2	S, T
C. eleusinoides Kunth	1	T
C. globosus All.	1	T
C. hyalinus Vahl	1	T
C. imbricatus Retz	1	T
C. melanospermus Valck.	2	B, F
C. nutans Vahl	2	Sw
C. odoratus L.	1	T
C. platystylis R. Br.	1	S
C. pumilus L.	2	F
C. rotundus L.	1	B, T
C. sesquiflorus Mattf. & Kük.	2	B
C. squarrosus L.	1	T
C. tenuispica Steud.	1	T
C. teneriffae Poir.	1	T
C. zollingerii Steud.	1	B
Datiscaceae:		
Tetrameles nudiflora R. Br.	2	L, Sw, S, W, T
Dilleniaceae:		
Dillenia pentagyna Roxb.	2	S, W, T
Tetracera scandens Merr.	2	F
Droseraceae:		
Aldrovanda vesiculosa L.	1	T

Drosera burmanni Vahl	1	S, F
D. indica L.	1	S
D. peltata Smith	1	B, L, T

Ebenaceae:

Diospyros buxifolia Hiern.	2	B
D. cauliflora Bl.	2	B, L
D. ebenum Koen.	1	W, T
D. ferrea Bakh.	1	Sw, F, W
D. hasseltii Zoll.	2	B
D. javanica Bakh.	3	B, L, S, F, T
D. malabarica Kostel.	2	Sw
D. maritima Bl.	1	L, F, W, T
D. montana Roxb.	1	L, S, T
D. sundaica Bakh.	3	B
D. toposia Ham.	2	Sw

Elatinaceae:

Bergia ammannioides Roth	1	T

Flacourtiaceae:

Casearia flavovirens Bl.	3	B
C. grewiaefolia Vent.	1	B, L, Sw, T
Homalium tomentosum Bth.	2	B, Sw, F, T
Pangium edule Reinw.	4	B, Sw
Ryparosa javanica Kurz.	2	B
Xylosma luzonense Clos	3	F, W. T
X. sumatranum Sloot.	3	B, L

Flagellariaceae:

Flagellaria indica L.	1	B, F, T

Gnetaceae:

Gnetum gnemon L.	1	S

Gramineae:

Arthraxon lanceolatus Hochst.	2	B, T
A. lancifolius Hochst.	2	B, L
A. quartinianus Nash	2	L, S
A. typicus Kds	3	B, F
Arundinella ciliata Miq.	2	T
A. humilior Jans.	2	S
A. pumila Steud.	2	L, T
A. setosa Trin.	2	B
Astenochloa tenera Buse	3	L, T
Bothriochloa ewartiana Hubb.	4	Sw, T
B. glabra Camus	1	S, T
B. modesta Back. & Henr.	3	B
B. pertusa Camus	2	Sw, S, T
Brachiaria fusiformis Reed.	3	T
B. holotricha Ohwi	3	S
B. lanceata Ohwi	3	W, T
B. ramosa Stapf	2	S, T
B. reptans Gardn. & Hubb.	1	S, A, T
B. villosa Camus	2	B
Brachyachne tenella Hubb.	4	S, T
Brachypodium sylvaticum Beauv.	2	B, L
Capillipedium arachnoideum Henr.	3	B, T
C. assimile Camus	2	Sw, F, T
C. parviflorum Stapf	1	B, F, T
Centotheca lappacea Desv.	1	T
Chloris barbata Sw.	1	B, L, Sw, T

C. incompleta R. & S.	2	Sw, T
C. truncata R. Br.	4	T
Chrysopogon aciculatus Trin.	1	Sw, T
C. subtilis Miq.	3	S
C. tenuiculmis Henr.	3A	L, S, T
Coelorhachis rottboellioides Camus	4	T
Cymbopogon procerus Domin.	4	T
C. rectus Camus	3	B, S
Cynodon arcuatus Presl.	2	B, T
C. dactylon Pers.	1	B, L, T
C. parviglumis Ohwi	1	T
Cyrtococcum accrescens Stapf	1	S, W, T
C. patens Camus	1	Sw, W, T
C. trigonum Camus	1	L
Deyeuxia australis Jans.	3	B, L, Sw
Dichantium annulatum Stapf	1	T
D. erectum Ohwi	3A	S, T
D. superciliatum Camus	4	T
Digitaria argyrostachya Fern.	3	B, L, S
D. eminens Back.	3	B
D. fuscescens Henr.	1	T
D. heterantha Merr.	2	B
D. junghuhniana Henr.	3	S
D. longiflora Pers.	2	S
D. microbachne Hitchk.	1	S, T
D. mollicoma Henr.	3	T
D. remota Henr.	3	B
D. timorensis Bal.	1	B, T
D. violascens Link.	2	Sw
D. virens Ridl.	3	S, T
Dimeria ornithopoda Trin.	1	B, S
Echinochloa colonum Link.	1	Sw, S, W, T
Elytrophorus spicatus Camus	1	L
Eragrostis cumingii Steud.	3	B, L, T
E. diarrhena Steud.	2	T
E. megastachya Link.	1	B, L, S, T
E. tenella R. & S.	1	L, S, T
E. warburgii Hack.	3	T
Eriochloa procera Hubb.	1	S, T
Eulalia fimbriata O.K.	2	B
Eu. fulva O.K.	4	F
Eu. leschenaultiana Ohwi	1	Sw, S, T
Eu. trispicata Henr.	1	B, S
Festuca nubigena Jungh.	3	L
Garnotia acutigluma Ohwi	2	B
Hackelochloa granularis O.K.	1	B, Sw, S, W, T
Heteropogon contortus R. & S.	1	B, Sw, S, F, A, W, T
H. triticeus Stapf	1	Sw, S, F, W, T
Hyparrhenia filipendula Stapf	1	S, F, T
Isachne beneckei Hack.	3	L
I. miliacea R. & S.	1	T
I. pangeranensis Z. & M.	3	B, L
I. pulchella R. & S.	2	S, T
Ischaemum barbatum Retz	2	S
I. muticum L.	1	B, S, W, T
I. rugosum Salisb.	2	Sw, T
I. timorense Kunth	1	L, Sw, S, T
Iseilema maculatum Jans.	3A	W
I. minutiflorum Jans.	3A	S
Leptaspis urceolata R. Br.	2	B
Leptochloa panicea Ohwi	1	T

Lepturus repens R. Br.	1	B, T
Microstegium ciliatum Camus	2	S, W, T
M. dispar Henr.	3	B, L
M. eucnemis Camus	2	T
M. montanum Henr.	2	Sw
Miscanthus floridulus Warb.	1	B
Mnesithea laevis Kunth	2	B
Muehlenbergia arisanensis Hay.	2	L
Neyraudia reynaudiana Hutch.	2	B
Ophiuros tongcalingii Elm.	1	B, Sw, S, F
Oplismenus burmannii Beauv.	1	B, W, T
O. compositus Beauv.	1	B, L, W, T
O. undulatifolius Beauv.	1	L
Panicum caudiglume Hack.	2	B, Sw, S, A, W, T
P. montanum Roxb.	2	Sw, S
P. trachyrhachis Benth.	4	T
Paspalidium flavidum Camus	2	L, Sw, S, T
P. geminatum Stapf	1	T
Paspalum auriculatum Presl.	2	F, T
P. cartilagineum Presl.	3	S, T
P. commersonii Lam.	1	Sw, S
P. longifolium Roxb.	2	Sw, S, T
P. orbiculare Forst.	4	F, T
Perotis hordeiformis H. & A.	2	B, L, S, F, W
P. indica O.K.	2	B
P. rara R. Br.	4	S, T
Phragmites karka Steud.	2	B
Pogonatherum paniceum Hack.	1	B, Sw, S, F, T
Polytrias amaura O.K.	3	B, Sw, T
Pseudechinolaena polystachya Stapf	1	L, W
Pseudopogonatherum contortum Camus	1	S
Rottboellia exaltata L. f.	2	B, T
R. formosa R. Br.	4	W, T
Saccharum spontaneum L.	2	B, T
Schizachyrium brevifolium Nees	1	B, S, T
Sch. fragile Camus	1	S, T
Sch. sanguineum Alst.	2	S
Sclerachne punctata R. Br.	3	B, S, T
Sehima nervosum Stapf.	1	B, S, W, T
Setaria adhaerens Chiov.	1	B, S, T
S. laxa Merr.	3	L, S, T
Sorghum laxiflorum Bailey	4	W, T
S. nitidum Pers.	1	S, T
S. timorense Buse	3	T
Spinifex littoreus Merr.	2	B, L, Sw, S, T
S. longifolius R. Br.	4	Sw, F, T
Sporobolus diander Beauv.	1	S, T
Sp. virginicus Kunth	1	B, S, T
Streblochaete longiaristata Pilg.	2	L
Thaumastochloa cochinchinensis Hubb.	2	B
Thelepogon elegans R. & S.	2	T
Themeda arguens Hack.	1	B, S, T
Th. australis Stapf	4	B, L, S, W, T
Th. intermedia Dur. & Jacks.	2	W, T
Tripogon exiguus Buse	2	B, L
Zoisia matrella Merr.	1	B

Lecythidaceae:

Barringtonia asiatica Kurz	1	B, Sw, T
B. racemosa Bl.	1	F, T
B. spicata Bl.	2	T

Planchonia alata Bl.	3A	T
P. valida Bl.	3	Sw, T
Leguminosae:		
Intsia bijuga O.K.	1	Sw, F, T
I. palembanica Miq.	2	T
Sophora glauca DC.	2	S, T
S. tomentosa L.	1	Sw
Loranthaceae:		
Amyema miraculosa Tiegh.	4	T
A. polytrias Dans.	3A	T
A. timorana Dans.	3A	T
A. tristis Tiegh.	3	B, F
Amylotheca stenopetala Dans.	3	F
A. triflora Dans.	3	Sw, S, F, T
Dendrophtoe falcata Ett.	1	T
Dicymanthes elliptica Dans.	3A	S
D. lombocana Dans.	3A	L
D. longipes Dans.	3A	B
Ginalloa arnottiana Korth.	3	L
Korthalsella dacrydii Dans.	3	T
Scurrula atropurpurea Dans.	3	B
S. obovata Don	3	L, Sw, S, T
Viscum articulatum Burm.	1	T
V. ovalifolium A. P. DC.	2	Sw, S, T
Melastomataceae:		
Astronia spectabilis Bl.	3	B, L
Medinilla crassifolia Bl.	3	B
M. javanensis Bl.	3	B
M. radicans Bl.	3	B, Sw
M. speciosa Bl.	3	B, L, F
Melastoma aculeolatum Bakh. f.	3A	T
M. balinense Bakh. f.	3A	B
M. caesium Bakh. f.	3A	Sw
M. curvisepalum Bakh. f.	3A	L
M. decipiens Bakh. f.	3A	B, S
M. elbertii Bakh. f.	3A	L
M. malabathricum L.	1	B, F, T
M. polyanthum Bl.	1	B, Sw, F, W, T
M. porphyreum Bl.	3	F
M. rufosetosum Bakh. f.	3A	L
M. trachyphyllum Back.	3	L
Memecylon oleaefolium Bl.	3	S
M. pauciflorum Bl.	1	Sw, T
M. pseudonigrescens Bl.	3	L
Omphalopus fallax Naud.	3	B
Osbeckia chinensis O.K.	1	B, L, T
O. dolichophylla Naud.	3	Sw, S
Otanthera cyanoides Tryana	3	Sw
Sonerila brachyandra Naud.	3	Sw
Myricaceae:		
Myrica esculenta Buch.-Ham.	2	B, L, S, F
M. javanica Bl.	3	B, L
Oxalidaceae:		
Biophytum fruticosum Bl.	2	W
B. petersianum Klotzsch	1	L
Pedaliaceae:		
Josephinia imperatricis Vent.	4	B, L, Sw, S, T

Plumbaginaceae:		
Aegialitis annulata R. Br.	4	F, A, T
Plumbago indica L.	2	Sw
P. zeylanica L.	2	T
Podocarpaceae:		
Podocarpus amara Bl.	4	B, L, Sw, S, T
P. imbricata Bl.	2	B, L, Sw, S, F, T
P. neriifolia Don	2	B, T
P. rumphii Bl.	3	S, T
Polygonaceae:		
Polygonum attenuatum R. Br.	4	S, T
P. barbatum L.	1	L, Sw, S, F, T
P. caespitosum Bl.	2	B
P. chinense L.	2	B, L, Sw, F, T
P. nepalense Meissn.	2	L
P. orientale L.	1	S, W
P. plebejum R. Br.	1	L
P. runcinatum Don	2	B, T
Rumex brownii Campd.	4	T
Pontederiaceae:		
Monochoria vaginalis Presl.	2	T
Portulacaceae:		
Portulaca quadrifida L.	2	T
Rubiaceae:		
Argostemma montanum Bl.	3	B
A. timorense Benn.	3A	T
Ixora balinensis Brem.	3A	B
I. brachycotyla Brem.	3A	B
I. longipes Z. & M.	3	T
I. nigricans W. & A.	2	B
I. paludosa Kurz.	3	L, Sw, S, T
I. sumbawensis Brem.	3A	Sw
I. timorensis Decne	3	S, F, T
Pavetta balinensis Brem.	3A	B
P. platyclada K. Sch.	3	Sw
P. reinwardtii Brem.	3	T
P. sumbawensis Brem.	3A	Sw, W, T
Wendlandia burkillii Cow.	3	Sw, T
Sapindaceae:		
Alectryon glaber Radlk.	3A	T
A. serratum Radlk.	3	Sw
Allophylus cobbe Bl.	2	B, L, Sw, F, W, T
A. ternatus Radlk.	4	T
Arytera xerocarpa Adelb.	2	T
Atalaya salicifolia Bl.	4	Sw, T
Dodonaea viscosa Jacq.	1	B, L, Sw, T
Elattostachys verrucosa Radlk.	3	L, T
Erioglossum rubiginosum Bl.	1	Sw, T
Guioa pleuropteris Radlk.	2	T
Harpullia cupanioides Roxb.	2	L, T
H. fraxinifolia Bl.	3A	T
Lepisanthes pallens Radlk.	3A	T
Mischocarpus fuscescens Bl.	2	Sw
M. sundaicus Bl.	1	Sw, W, T
Otophora fruticosa Bl.	3	Sw
Pometia tomentosa T. & B.	2	W. T

Sapindus balicus Radlk.	3A	B, L
S. rarak DC.	2	L
Schleichera oleosa Merr.	2	B, Sw, S, A, W, T
Tristiropsis canarioides Boerl.	3	T
Sapotaceae:		
Lucuma luzoniensis H. J. Lam	3	B
L. macrantha H. J. Lam	3	Sw
Madhuca burckiana H. J. Lam	3	Sw
Manilkara kauki Dub.	1	B, Sw
Mimusops elengi L.	1	B, L, F, W, T
Palaquium amboinense Burck	3	Sw
P. javense Burck	3	B
P. obovatum Engl.	2	Sw
P. obtusifolium Burck	3	B, Sw, F
Planchonella firma Dub.	3	F, W
P. moluccana H. J. Lam	3	F
P. nitida Dub.	2	S, F, W, T
P. obovata H. J. Lam	1	S, F, W, T
P. obovoidea H. J. Lam	3	F, T
P. oxyedra Dub.	3	F, T
Sarcospermaceae:		
Sarcosperma paniculatum Stapf & King	3	F
Scrophulariaceae:		
Wightia borneensis Hk. f.	3	Sw, F
Sonneratiaceae:		
Duabanga moluccana Bl.	3	B, L, Sw
Sonneratia alba J. E. Sm.	1	B, F, W, T
S. caseolaris Engl.	1	T
Stylidiaceae:		
Stylidium javanicum Sloot.	3	S
Taccaceae:		
Tacca palmata Bl.	3	F, T
T. pinnatifida Forst.	1	S, W, T
Theaceae:		
Adinandra javanica Choisy	3	L, Sw, F
Typhaceae:		
Typha angustifolia L.	1	T
Umbelliferae:		
Centella asiatica Urb.	1	B, A, T
Oenanthe javanica DC.	1	B
Pimpinella javana DC.	3	B, L
Sanicula europaea L.	2	B
Trachymene acerifolia Norm.	3	F, T
Urticaceae:		
Elatostema parvum Bl.	2	L
E. rostratum Hsk.	3	L
Procris pedunculata Wedd.	2	B, T
P. ruhlandii Schröt.	3A	B
Zygophyllaceae:		
Tribulus cistoides L.	1	B, L, Sw, S, F, A, T

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EPIPACTIS HELLEBORINE, A PROBLEM OF NOMENCLATURE

BY

P. VERMEULEN

(*Hugo de Vries Laboratorium, Amsterdam*).

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In the Netherlands two forms of the Broad-leaved Helleborine occur, the form of the sand-dunes, which is called *Epipactis helleborine* var. *neerlandica* and the inland-form *E. helleborine* var. *helleborine*. Mr. J. H. Stock, biol. cand., established the differences between these two in a statistical way and his studies prompted me to write this article. First Mr. Stock asked the Linnean Society for the photographs of the species of *Serapias Helleborine latifolia* from the Linnean herbarium and the secretary was kind enough to send the pictures. Our amazement on receiving these may be imagined, for it appeared that *Serapias Helleborine latifolia* of Linnaeus was not the Broad-leaved Helleborine but the Marsh Helleborine! With this a problem arose: Would it be necessary in future to use the epithet *helleborine* for the Marsh Helleborine and to change the name of the Broad-leaved Helleborine? This would be very undesirable and I have tried to avoid this change of names.

This was the beginning of a historical review of the opinions of the authors of the old herbals, and of Linnaeus and his contemporaries on *Serapias*, *(H) Elleborine* and *Epipactis* and on other names used for these plants. When pictures were given in their works it was easier to pass judgment on their opinion. It appeared, however, that in different herbals pictures were given copied from one original, sometimes mutilated, and so different figures copied from plates of the same species were cited for different species. Not all the pictures were equally good and sometimes a figure was compiled from two different plants. This is the case with *Epipactis latifolia* from Besler's Hortus Eystettensis (1613). The habit of the plant is a Helleborine but the spike may be that of *Platanthera bifolia* for the flowers have long slender spurs! We find the same picture copied in Morison's Plant. Hist. Oxoniensis, 1699, (section 12, tab. II, Fig. 1 or 11) with the name *Helleborine latifolia montana* used by Caspar Bauhin in his Pinax.

The plant depicted by Camerarius in his De plantis Epitome utilissima, 1586, which is a good Marsh Helleborine, is copied in Morison's work as Fig. 4 of the same tab. sub *Helleborine montana angustifolia spicata* but the figure is not satisfactory. A good picture of the Marsh Helleborine is also found in Pemptades of Dodonaeus under the name *Helleborine* and we find the same woodcut in Clusius' Historia but here the lower half only of the lower leaf is shown, the upper part has disappeared! In Morison's work the same figure is copied again but now the whole lower leaf is missing (Tab. II, Fig. 7). The Marsh Helleborine has a hairy stem but in the wood-cut of Dodonaeus no hairs are shown, whereas in the copper-plate of Camerarius they are. This is the reason why in Morison's work the same species, the Marsh Helleborine, is pictured as a hairy plant (copied from Camerarius) and as a smooth plant (copied from Dodonaeus) with two different names: *Helleborine montana angustifolia spicata* and *Helleborine angustifolia palustris sive pratensis*. This causes confusion!

It is a striking fact that most of the figures depicted give the Marsh Helleborine. An exception is found in Bauhino & Cherlero Historiae Plantarum Universalis, in which in tom. III (1651) p. 516 under *Elleborine dodonaei* the Broad-leaved Helleborine is figured and under *Damasonium alpinum sive Elleborine, floribus albis*, we see the Marsh Helleborine again. The figure in the French translation of Dalechamps is a Helleborine as to the habit, but the flowers are badly represented and are not determinable.

In the work of Vaillant (1727) not a single figure of *Helleborine* is given but the descriptions are good and give the impression that Vaillant knew the plants very well.

In Linnaeus' work we find the first description of a plant of the group of the Helleborines in Hortus Cliffortianus (1737) without a figure. The herbarium as made by Linnaeus is now in the British Museum. It contains a single herbarium specimen of *Serapias* which is a Marsh Helleborine. The diagnosis is very short but several synonyms are enumerated and four varieties are distinguished:

Serapias g. pl. 683.

p. 429:
SERAPIAS caule multifolio multifloro.
Helleborine latifolia montana. *Bauh. pin.* 186. *Moris. hist.* 3. *p.* 486 *s.* 12, *t.* II. *f.* 11 (*male*) 12. 4. 7.
Helleborine recentiorum. 3. *Clus. hist.* 1. *p.* 273.
Helleborine. *Dod. pempt.* 384.
Elleborine dodonaei. *Bauh. hist.* 3. *p.* 516.
Sigillum sanctae mariae. *Caesalp. syst.* 431.

p. 430:
α Helleborine angustifolia palustris sive pratensis. *C. B.*
β Helleborine flore carneo. *C. B.* 187.
γ Helleborine altera, atro-rubente flore. *C. B.* 186.
δ Helleborine palustris nostras. *Raj. hist.* 1231.
Crescit in locis sterilibus opacis & desertis sat frequens per *Europam.* Species haec a Botanicis maxime multiplicata est, hinc qui species plures desiderant, ut eas structura vera diversa florum demonstrant

necesse est; huc usque certe nulla nota specifica in hoc genera descripta est.

The first synonym, that of C. BAUHIN, includes not only the bad figure of the Broad-leaved Helleborine with the flowers with spurs but also fig. 12, which is *Cephalanthera*, and the figs. 4 and 7 which represent the Marsh Helleborine. The synonym of CLUSIUS also stands for this plant and so does *Helleborine* of DODONAEUS, but the *Elleborine dodonaei* is the Broad-leaved Helleborine. *Sigillum sanctae mariae* of CAESALPINUS is a plant with a few white flowers and may be a *Cephalanthera*.

Of the four varieties the first is the name of fig. 7 of MORISON and the Marsh Helleborine and this is also var. δ. The vars β and γ are forms of the Broad-leaved Helleborine.

It seems that the varieties are borrowed from literature and are not based on personal observation. This also goes for the eleven vars enumerated in Acta Upsaliensis, 1740 (edited in 1744), in which LINNAEUS gives a survey of the Species Orchidum:

SERAPIAS

Serapias bulbis fibrosis, nectarii labio obtuso, petalis breviore.
Serapias caule multifolio multifloro. *Hort. Cliff.* 429.
Helleborine latifolia montana, *Bauh. pin.* 186. *Moris. hist.* 3. *p.* 486 *s.* 12. t. II. f. 1.
Helleborine barba rubra. *Riv. irr.*
Helleborine recentiorum II. *Clus. hist.* I. *p.* 272. *descr.*
Helleborine. *Dod.* 380. *Dalech. hist.* 1321.
Helleborine s. Epipactis recentiorum. *Lob. ic.* 312.
Elleborine Dodonaei. *Bauh. hist.* 3. *p.* 516.
Epipactis s. Elleborine. *Cam. epit.* 889. *fig. bona.*
Epipactis latifolia. *Besl. Eyst.*
α Helleborine flore albo. 1. Damasonium montanum latifolium. *Bauh. pin.* 187. *Moris. hist.* 3. *p.* 488. *s.* 12. *t.* II. f. 12.
Helleborine albo flore. *Tabern. ic.* 724.
Damasonium alpinum s. Elleborine floribus albis *Bauh. hist.* 3. *p.* 516.
Damasonium. *Riv. irr.*
Epipactis angustis foliis. *Besl. Eyst.* 130. *fig. bon.*
β Helleborine latifolia, flore albo clauso. *Raj. syn.* 3. *p.* 384.
γ Helleborine ex albo sublutea. *Bauh. hist.* 3. p. 517. *Moris. hist.* 3. *p.* 487.
δ Helleborine flore carneo. *Bauh. pin.* 187.
Elleborine III. *Clus. pan.* 275. *vel.* IV. *Clus. hist.* I. *p.* 273.
ε Helleborine montana angustifolia spicata. *Bauh. pin.* 187. *Moris. hist.* 3. *p.* 487. *s.* 12. *t.* II. *f.* 4.
Helleborine IV. *Clus. pan.* 275. *vel.* V. *Clus. hist.* I. *p.* 273.
ζ Helleborine montana angustifolia purpurascens. *Bauh. pin.* 187. *Moris. hist.* 3. *p.* 487. *s.* 12. *t.* II. *f. ult.*
Helleborine recentiorum V. *Clus. pan.* 276.
Damasonium purpureum dilutum s. Elleborine IV. Clusii. *Bauh. hist.* 3. *p.* 516.

Damasonium alpinum. *Dalech. hist.* 1058.
Damasonium flore rubro. *Rupp. Jen.* I. *p.* 277.
Sigillum S. Mariae. *Caesalp. syst.* 341.
η Helleborine altera, atrorubente flore. *Bauh. pin.* 186.
ϑ Helleborine foliis praelongis angustis, floribus candidis. *Vaill. Paris.* 97.
Helleborine angustifolia, flore niveo. *Comm. hort.*
ι Helleborine palustris, angustifolia, flore albo. *Moris. hist.* 2. *p.* 468.
ϰ Helleborine palustris nostras. *Raj. hist.* 1231.
Helleborine palustris s. pratensis nostras, radice repente. *Moris. hist.* 3. *p.* 487.
λ Helleborine angustifolia palustris s. pratensis. *Bauh. pin.* 187. *Moris. hist.* 3. *p.* 487. *s.* 12. *t.* II. f. 7.
Helleborine recentiorum II. *Clus. pan.* 275. *vel* III, *Clus. hist.* I. *p.* 273.
Damasonium flore herbaceo intus non nihil candicante. *Bauh. hist.* 3. *p.* 517.
μ Helleborine pratensis angustifolia, flore herbaceo Lutetianorum. *Tournef. inst.* 436.
Helleborine herbaceo flore. *Moris. blaes.* 270.
Habitat in Europae collibus asperis graminosis duris, vel humentibus.

Serapias has now an other diagnosis: *Serapias bulbis fibrosis, nectarii labio obtuso, petalis breviore.* The labellum is indicated by LINNAEUS as a "nectarium" and the lip of the nectarium is probably the epichilium; actually this is obtuse in the Marsh Helleborine and shorter than the other petals. After *Helleborine latifolia montana* of C. BAUHIN only one fig. of MORISON is given: fig. (1 or) 11, that is the compilated figure.

The var. α comprises *Helleborine flore albo* and here fig. 12 of MORISON is given, that is *Cephalanthera;* the two synonyms of BAUHIN's Historia, however, *Damasonium alpinum* s. *Elleborine floribus albis* are the Marsh Helleborine again and according to VAILLANT *Epipactis angustis foli is* Besl. Eyst. 130, *fig. bon*, is a *Cephalanthera.* I did see the figure from the copy of BESLER's work at Leiden (library of the University, ed. 2) and it is a good figure of *Cephalanthera damasonium* (Mill.) Druce. The Amsterdam copy, ed. 1, however, does not contain this figure.

Later on in Species Plantarum, 1753, we met with the var. δ *Helleborine foliis praelongis angustis, floribus candidis* of VAILLANT, which is a *Cephalanthera* and with *Helleborine palustris nostras* and *Helleborine angustifolia palustris s. pratensis* which are the Marsh Helleborine.

From the enumeration of the varieties and the synonyms arranged under them, it follows that the genera *Epipactis* and *Cephalanthera* in the modern sense are reckoned among *Serapias.* Here we have therefore a collective species!

During the journeys to Oeland and Gotland in 1741 which are described in his itinerary LINNAEUS renewed the acquaintance with the Helleborines.

On June 18, 1741 (June 29 by modern standards, for the Gregorian calender was introduced in Sweden as late as 1753 and this makes a difference of 11 days, as Mr. Bengt Pettersson wrote to me) LINNAEUS found a plant at the Northwestern point of Oeland, which he had not seen before and of which he writes that it had not been found in Sweden: *Serapias Helleborine radicibus fibrosis, nectarii labio obtuso petalis breviore, foliis ensiformibus*, which was growing in the forest. In this place, according to Rikard STERNER's *Flora der Insel Öland* (1938) fig. 101, *Cephalanthera longifolia*, as the name of the species is now, still occurs and it seems probable that Linnaeus found it there in 1741. The plant is described on p. 144 and this citation is found in all LINNAEUS' later works! On June 28 (July 9) LINNAEUS was in Gotland (p. 196) and there he finds *Serapias, quae Helleborine latifolia montana* with nodded flowerspikes and with the flowers not yet opened. Later on, on July 2nd (July 13), LINNAEUS describes the flowers of the same species and now the flowerspikes were stretched. Of the two innermost petals the colour was pink and the lip was divided into three parts, the lateral parts of which were upright, somewhat pointed and with red stripes, whereas the middle part of the lip was heartshaped, not incised, white with a spot at the base which was heartshaped elevated and with three tips. It is not easy to decide what plant is meant here, but it seems most likely that the description suits the Marsh Helleborine best, especially because of the two lateral parts of the lip, for only this species has red stripes on these parts. On July 3rd (July 14) on p. 230 of the itinerary LINNAEUS mentions still an other *Serapias* with a single flower: *Serapias flore rubro* but perhaps this was a plant of which only a single flower was open and was really the Dark Red Helleborine (or the Red Helleborine?). The five petals had the same size and colour and the lip forms a sphere, which was somewhat contracted at the outside and with an elevated heartshaped spot. Because the place where this plant was found (Torsburg) is a limestone mountain, the Dark Red Helleborine could be expected there. The plant was rather different from that found on July 2nd because all the petals had the same size and colour. Mr. Bengt Pettersson wrote to me that the Swedish botanists believe that this plant was indeed the Dark Red Helleborine. On July 8 (19) and 20(31) resp. on p. 253 and p. 299 of the itinerary Serapias is found again but later on these pages are not cited by LINNAEUS as opposed to the former three.

In 1745 LINNAEUS published his Flora suecica, in which on p. 263–264 sub no 734 we find:

Serapias bulbis fibrosis, nectarii labio obtuso petalis breviore. *Act. ups.* 1740 *p.* 21
Serapias caule multifolio multifloro. *Hort. cliff.* 429.

α Helleborine floribus ex viridi & purpureo variis, labello acuminato, foliis brevissimis. *Hall. helv.* 275.
Helleborine latifolia montana. *Bauh. pin.* 186.
Epipactis sive Helleborine. *Cam. epit.* 889.

β Serapias radicibus fibrosis, nectarii labio obtuso petalis breviore, foliis ensiformibus. *Act. stockh.* 1741. *p.* 208. *It. oel.* 144.
Helleborine foliis praelongis angustis acutis. *Raj. syn.* 3. *p.* 384.

Helleborine longifolia, floribus magnis paucis albisque. *Hall. helv.* 275. *Habitat α in collibus pratorum* Roslagiensium *Borstelae, Hokhufwud etc. rarius; β in* Oelandia, *paroecia Boda, inter pagum Torp* & *septentrionalem terrae angulum, in densa sylva.*
Obs. *Nectarii labellum cordatum, reflexum.*

It seems that Linnaeus here divided the species into two varieties of which α comprises the Broadleaved Helleborine and the Marsh Helleborine as well. Var. β seems to represent the genus *Cephalanthera*. While Linnaeus described the lip of the species as "obtuso", Haller speaks of "labello acuminato"!

In Linnaeus' most important work, where he uses the binary nomenclature for the first time, his Species Plantarum, Linnaeus gives the following diagnosis (see vol. II, p. 949):

Helleborine 1. Serapias bulbis fibrosis, nectarii labio obtuso crenato petalis breviore. *Act. ups.* 1740. *p.* 21. *Fl. Suec.* 734. *It. oel.* 144. *It. Gotl.* 225, 197, 230. *Dalib. paris.* 276.

latifolia. Serapias caule multifolio multifloro. *Hort. Cliff.* 429. *Gmel. sib.* p. 8.
Helleborine latifolia montana. *Bauh. pin.* 186.
Epipactis s. Helleborine. *Cam. epit.* 889.
Helleborine flore carneo. *Bauh. pin.* 187.
Helleborine montana angustifolia spicata. *Bauh. pin.* 187.
Helleborine montana angustifolia purpurascens. *Bauh. pin.* 187.
Helleborine altera, atrorubente flore. *Bauh. pin.* 186.

longifolia ζ Serapias radicibus fibrosis, nectarii labio obtuso petalis breviore, foliis ensiformibus. *It. oel.* 144.
Helleborine foliis praelongis angustis, floribus candidis, *Vaill. paris.* 97.

palustris η Serapias angustifolia tomentosa, floribus herbaceis intus albis. *Sauv. monsp.* 42.
Helleborine palustris s. pratensis nostras. *Moris. hist.* 3. *p.* 487. *Raj. hist.* 1231.
Helleborine angustifolia palustris s. pratensis. *Bauh. pin.* (1)87.
Habitat in Europae asperis. 4
Limites inter latifoliam & longifoliam & palustris non reperi, diversitatem vidi.

The second species of this genus is *Serapias lingua* from the Mediterranean area.

Besides the use of the epithet *Helleborine* with which the collective species is indicated, there is still another fact that strikes us: while in Acta Upsal. many varieties are enumerated, here Linnaeus lumps a great many of them and only leaves three! There is a difference between the epithet of the species *Helleborine*, which is *italicized* and the names of the varieties which are not.

If we try to determine with the help of the earlier work of Linnaeus and the works cited, which plants are meant by the three varieties, we are helped by the characters, which LINNAEUS used for the latter two: the same which we found in Acta Upsaliensis but lumped with others.

The variety *latifolia* comprises not only the Marsh Helleborine from the Hort. Cliff., *Epipactis* of CAMERARIUS and *Hell. montana angustifolia spicata* Bauh., which are all the same, but also *Helleb. latifolia montana*, *Hell. flore carneo* and *Hell. altera, atrorubente flore* all indicating the Broad-leaved Helleborine or its allies.

Longifolia indicates *Cephalanthera* in its present meaning.

The third var. *palustris* is based on the work of SAUVAGE, which in my opinion is again the Marsh Helleborine and so are the other two quotations.

In spite of the fact that LINNAEUS saw different plants on his journeys he does not see the dividing lines between the varieties, but he sees differences! All together form one single species: *Serapias Helleborine* but even of the three varieties LINNAEUS has not got a good idea, for the var. *latifolia* comprises both the Marsh Helleborine and the Broad-leaved H. and the first is again represented by the var. *palustris*.

If we look at the herbarium specimens of LINNAEUS this is demonstrated again, for *Serapias Helleborine latifolia* is the Marsh Helleborine as the photograph showed (Fig. 1.) The second sheet is the same but LINNAEUS wrote the word *alba* on it, I suppose because it was a white flowering plant. LINNAEUS does not see the difference between *latifolia*, *longifolia* and *palustris* on the level of genera, or even on that of species. He will later on when he is forced to do so under the influence of other authors.

In 1755 follows the second edition of Flora suecica, in which on p. 318 we find a treatise of the genus *Serapias* with a single species again (see no 819):

SERAPIAS (*Helleborine*) bulbis fibrosis, nectarii labio obtuso petalis breviore. *Act. Ups.* 1740, *p.* 21. *Fl. suec.* 734. *Spec. plant.* 949.
Serapias caule multifolio multifloro. *Hort. cliff.* 429. *Gmel. sib.* 1. *p.* 8.
Helleborine latifolia montana. *Bauh. pin.* 186.
Epipactis sive Helleborine. *Cam. epit.* 889.
β Serapias radicibus fibrosis, nectarii labio obtuso petalis breviore, foliis ensiformibus. *Act. stockh.* 1741 *p.* 208, *It. oel.* 144.
Helleborine foliis praelongis angustis acutis. *Raj. angl.* 3. p. 384.
Helleborine longifolia, floribus magnis paucis albisque. *Hall. helv.* 275.
Habitat α in collibus Rostlagiensium *Borstelae*, Hokhufwud *etc. rarius, inque* Gotlandia 299, Scania 301; *β in* Oelandia 145, *paroecia Boda, inter pagum Torp & septentrionalem terrae angulum, in densa sylva.* 4.
Nectarii labellum cordatum, reflexum.
Diversae plantae descriptae videantur. Gotl. 225, 196, 230. Oel. 145 *non mihi constant notae internae per quas distinguantur.*
Caulis in hisce nutat ante florescentiam; in β folia ovata, in α ensiformia & huic flos petalis longioribus.

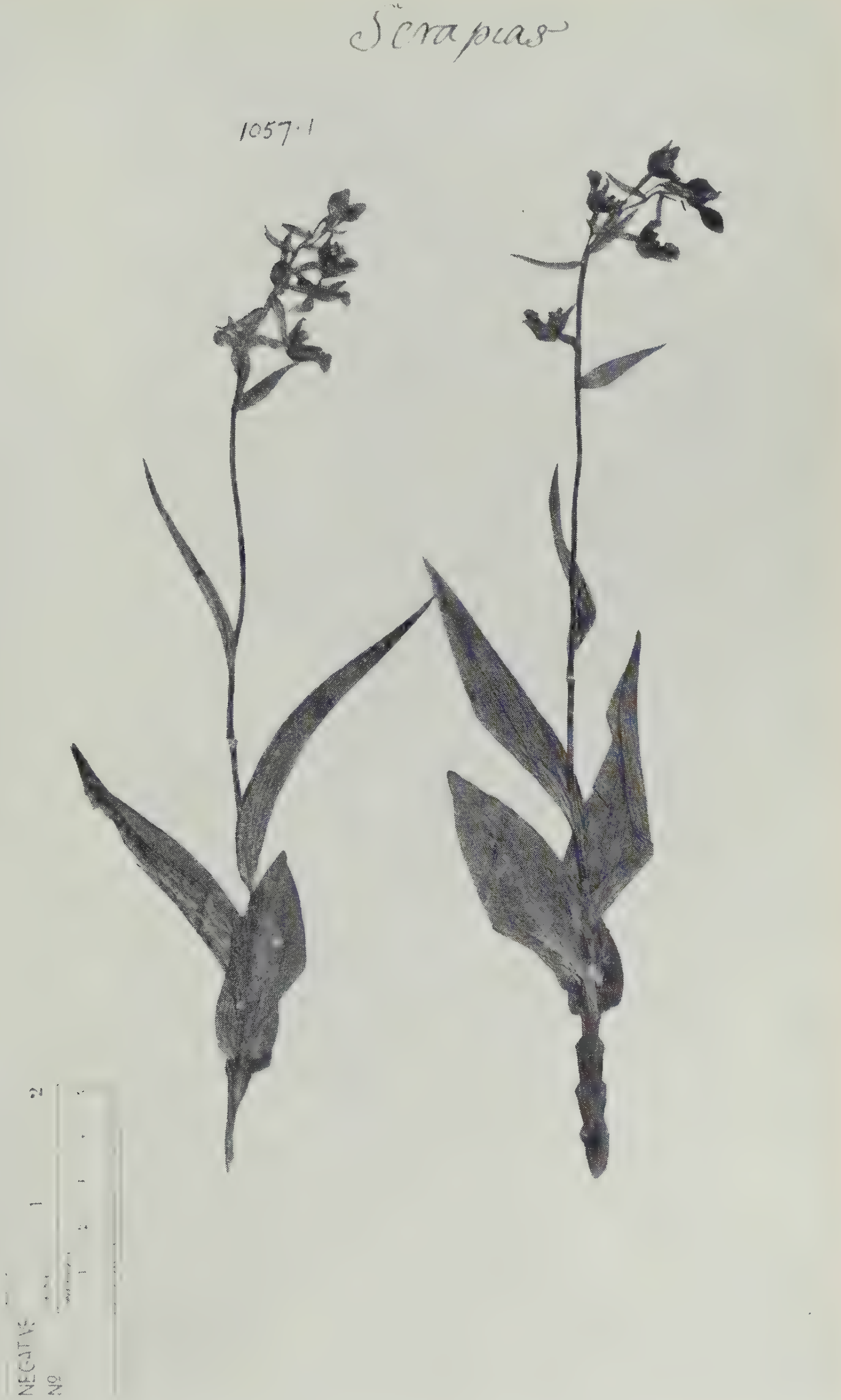

Fig. 1. *Serapias Helleborine latifolia.* Sheet with two specimens out of Linnaeus' herbarium.

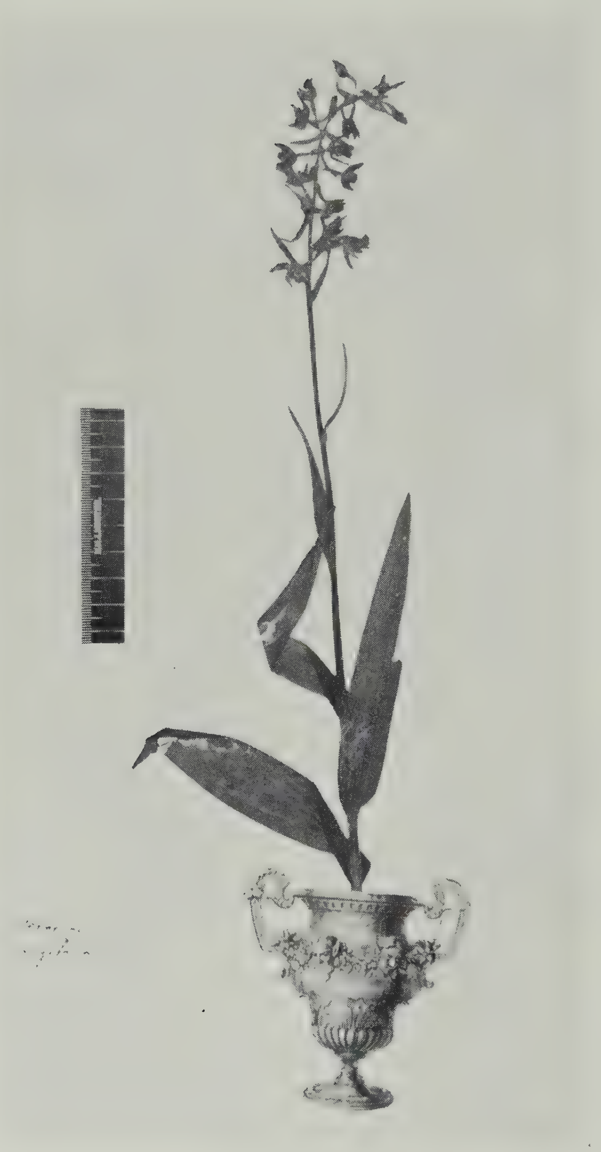

Fig. 2. *Serapias longifolia* L. (non *S. longifolia* Huds.). Sheet from the Hortus Cliffortianus Herbarium, British Museum, London.

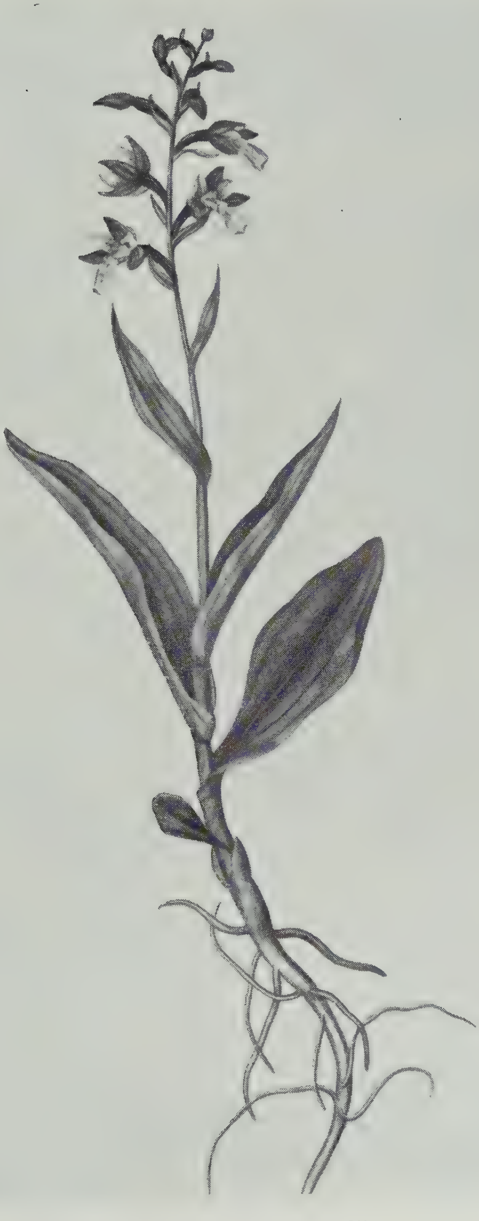

Fig. 3. Flora danica, tab. 267.
Type of Epipactis palustris (Mill.) Crantz.

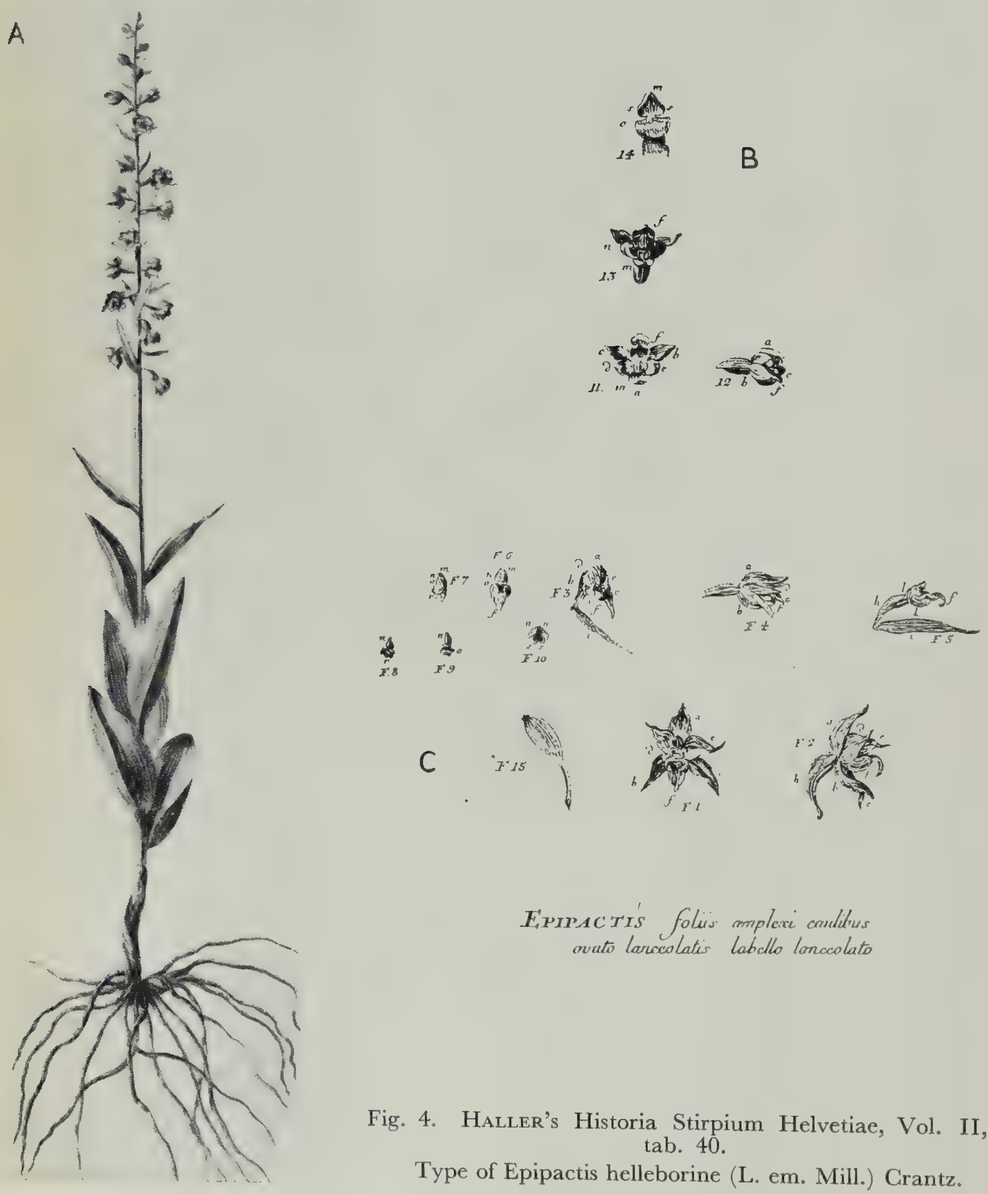
A
14
B
13
11.
12
F 6
F 7
F 3
F 4
F 5
F 8
F 9
F 10
C
F 15
F 1
F 2
EPIPACTIS foliis amplexi caulibus
ovato lanceolatis labello lanceolato

Fig. 4. HALLER's Historia Stirpium Helvetiae, Vol. II, tab. 40.
Type of Epipactis helleborine (L. em. Mill.) Crantz.

The letter a is probably erroneously omitted for it is mentioned in the text, but perhaps LINNAEUS meant to say with this that var. a is the species itself, for in *Viola* (tricolor) the a is not mentioned either. It is a remarkable fact that the leaves of a are called " ovata" while those of *Cephalanthera* are "ensiformia". By "ovata" are meant the leaves of the Marsh Helleborine, I suppose, but the leaves of this species are often rather narrow, as we can see in the specimens of LINNAEUS' herbarium.

In this work too *Serapias Helleborine* is a single, collective species but the work of HUDSON, Flora anglica, strikes a new note. In 1762 this author distinguishes two species in *Serapias:*

1. *latifolia* SERAPIAS bulbis fibrosis, nectarii labio obtuso petalis aequali, fructibus pendulis.
2. *longifolia* SERAPIAS bulbis fibrosis, nectarii labio obtuso petalis breviore, fructibus erectis.

With this the epithet *longifolia* Huds. is established for *Cephalanthera* for this genus has the fruits upright. In this work var. *grandiflora* is mentioned but does not reach the level of a species.

Obviously LINNAEUS read HUDSON's work and appreciated it for in the second edition of Species Plantarum, 1763, he follows HUDSON's lead. In this work LINNAEUS describes also two species of the Mediterranean area, which we still know as belonging to the genus *Serapias,* as altered by SWARTZ.

Four species are distinguished now:

1 *Serapias Helleborine:*
bulbis fibrosis, floribus erectis bractea brevioribus.
Serapias bulbis fibrosis, nectarii labio obtuso crenato petalis breviore. *Act. ups.* 1740 *p.* 21. *Fl. suec.* 734; 819. *It. oel.* 144. *It. gotl.* 225, 197, 230. *Dalib. paris.* 276.
latifolia α Serapias caule multifolio multifloro. *Hort. cliff.* 429. *Gmel. sib.* I p. 8.
Helleborine latifolia montana. *Bauh. pin.* 186.
Epipactis s. Helleborine *Cam. epit.* 889.
β Helleborine flore carneo. *Bauh. pin.* 187.
Habitat in Europae asperis. 4.
2 *Serapias lingua*, which still has the same name nowadays, and so has:
3 *Serapias cordigera*, but then follows
4 *Serapias longifolia:*
bulbis fibrosis, floribus erectis, bractea longioribus. Serapias radicibus fibrosis, nectarii labio obtuso breviore foliis ensiformibus. *It. oel.* 144.
β Helleborine angustifolia palustris s. pratensis, *Bauh. pin.* (1)87.
γ Helleborine palustris s. pratensis nostras. *Raj. hist.* 1231. *Moris. hist.* 3. p. 487.
δ Helleborine flore albo s. Damasonium montanum latifolium. *Bauh. pin.* 187.
Helleborine montana angustifolia spicata. *Bauh. pin.* 187.
Helleborine montana angustifolia purpurascens. *Bauh. pin.* 187.

> Habitat in Europa.
> Affinis maxime S. Helleborinae, sed huic petala lanceolata: nec ovata. Spica ante florescentiam nutans; corolla major coloratior. Bracteae flore longiores; illi vero exceptis sibiticis, vix ac vix.

From this we may conclude that LINNAEUS was not able at the time to distinguish the species of our genera *Epipactis* and *Cephalanthera*. The only difference between the diagnoses of nos. 1 and 4 is the length of the bracts. While var. α (the species) of no. 4 is our *Cephalanthera* (*It. oel.* 144), var. β, a synonym taken from BAUHIN, is a Marsh Helleborine and var. γ is the same species but var. δ is *Cephalanthera* again. The nodded flowerspike applies in the case of Marsh- and Broad-leaved Helleborine but not in the case of *Cephalanthera*. Here parts of different species are combined into one. Only if we exclude the vars β and γ the rest would suit this genus except for the nodded flowerspike!

LINNAEUS was inaccurate also in citing *It. oel.* under the first species, whereas it belongs under *longifolia* where it is found too. Only the var. *latifolia* remains, the var. β is not named Not only does the var. *longifolia* cease to exist but also the var. *palustris*, probably because both are incorporated in the new species *Serapias longifolia*. However, we see that in *S. Helleborine* and in *S. longifolia* as well synonyms are cited, which belong to the Marsh Helleborine. Summarizing we can say that:

1 *Serapias Helleborine* is Marsh- and Broad-leaved Helleborine and
2 *Serapias longifolia* is *Cephalanthera* and Marsh Helleborine!

From this it appears again that LINNAEUS was not able to distinguish the species as we do now!

In the meantime, in 1760, Albert von HALLER, the famous Swiss botanist, published a paper in Acta Helvetica, vol. IV, pp. 82–166, entitled: *Orchidum Classis Constituta*, in which he gives a clear description of the species in the genus *Epipactis*, as he now called it, and here we find as no 2 the species now known as *Cephalanthera rubra* and sub no 3 a species is mentioned: *Epipactis caule folioso pauciflora, lineis in obtuso labello levibus* with the var. *a Latifolia folii ovato lanceolatis* and var. β *Foliis angustis lanceolatis, quales in rubra sunt, floribus candidis, labello luteolo, qua parte lineatum est*, both forming together our white flowering *Cephalanthera*. As a synonym is given LINNAEUS' Oel. resa p. 144. Under no 4 we find (pp. 108–109): *Epipactis foliis amplexicaulibus ovato lanceolatis, labello lanceolato*, and translated the description runs as follows:

> the three outer, somewhat greenish, petals on a smaller flower, firmer than with the foregoing species, ovate-lanceolate, somewhat hairy on the outside. The two innermost a little bit shorter and narrower, white with a greenish tint. The hood is longer than the sixth petal, so that the lip does not project and therefore is not any longer than the two outermost lower petals. Of the lip the first part is a small boat, hollow below, resembling a spur and covered by a greenish glue substance and with white margins.

> The rest (coulter) is separated from the boat (*cymba*) by a constriction on both sides. Coulter (*vomer*) descending, nearly heart-shaped, short with the margin reflexed, with its base connected with the boat. In the beginning of this "bract" a heart-shaped figure is found with a sharp margin upright; the other part of the coulter has no undulating lines, it ends pointed, usually bent upwards. It is white and the lip is reddish and the whole flower and the colour of the boat become, as they get older, more and more purple and brown as in Orchis . . . . and when out of flower reddish lines appear on the tip of the lip.

This description is clear enough to establish that it suits the Broad-leaved Helleborine. The hypochilium is indicated as boat (cymba), the epichilium somewhat unusually as coulter (vomer). Three varieties are distinguished:

> α Flore viridi & albescente, plante nempe junior.
> *Elleborine recentiorum genus* II CLUS. *Pann.* L. II c. 33. p. 275.
> *Helleborine latifolia montana* C. BAUHIN. *Pin. Basil.*
> β Flore purpureo & carneo dilutiori.
> *Elleborine recentiorum genus* III. CLUS. *Pannon.* p. 276.
> γ Flore & inprimis unguine, quod in cymba est labelli, atrorubente; serotina, atque praelongo spica.
> *Helleborine altera flore atrorubente*, C. B. *Phytopin.* p. 342. *Pin.* Basil.

All three are nearly the same, without large differences. The latter is the Red-Brown Helleborine, but this species, as we distinguish it now, is earlier in flower than the Broad-leaved species, not later.

No. 5 of HALLER is: *Epipactis foliis ensiformibus, floribus pendulis, labello obtuso, per oras plicato* with, as to the flower, the following description (p. 111/112):

> Striking, wide opened flower. The three outer petals, ovate-lanceolate, somewhat hairy, green mixed with purple or purple, and dull on the outside. The two inner petals shorter, more blunt and finer, white with light-purple. The sixth petal more extending than in the other species of Epipactis and the longer part of the lip extends like a coulter. There is a boat on both sides with an appendix like upright oval wings adorned with purple lines, yellow spots and separated from the other coulter-shaped part by deep incisions. On this "bract" at the beginning of the coulter two yellow knobs. This part itself is heart-shaped, but obtuse, incised on both sides, which is characteristic for this species only, white, folded and as it were serrated.

As synonyms we find on p. 113:

> *Helleborine angustifolia palustris vel pratensis* C. B. *Phytopin.* p. 342, *Basil.* p. 55. *Pin.*
> *Helleborine angustifolia* RAII *Cantabrig. p.* 72. Prima bona descriptio.

Especially the upright wings of the hypochilium are very characteristic for the Marsh Helleborine and also the rest of the description leaves no doubt which plant was meant by Haller.

Linnaeus' reaction on this clever work followed in 1767 in the 12th edition of Systema Naturae. In vol. II pp. 593/594 we read:

1012 SERAPIAS. *Nectarium* ovatum, gibbum, labio ovato.

latifolia. 1. S. bulbis fibrosis, fol. ovatis amplexicaulibus, flor. pendulis. *Fl. suec.* 819. Serapias bulbis fibrosis, nectarii labio obtuso crenato petalis aequali, fructibus pendulis. *Huds. angl.* 341. Serapias bulbis fibrosis, floribus secundis, labello planiusculo, petalis ovatis. *Scop. carn.* 255. Serapias bulbis fibrosis, caule multifloro, floribus spicatis, nectarii labio petalis breviore. *Ger. prov.* 132. Epipactis foliis amplexicaulibus ovato-lanceolatis, labello lanceolato. *Hall. act. helv.* 4. *p.* 108. Epipactis s. Helleborine. *Cam. epit.* 187. Helleborine floribus e viridi & purpureo variis labello acuminato, foliis brevissimis. *Hall. helv.* 275. Helleborine latifolia montana. *Bauh. pin.* 186. *Folia amplexicaulia. Spica multiflora, longa. Petioli longi. Flores fructusque penduli. Nectarium lineis nullis.*

longifolia. 2. S. bulbis fibrosis, fol. ensiformibus sessilibus, flor. pendulis. Serapias bulbis fibrosis, nectarii labio obtuso longitudine petalorum. *Ger. prov.* 132. Serapias bulbis fibrosis, floribus sparsis patulis, labello concavo petalis longiore. *Scop. carn.* 256. Epipactis foliis ensiformibus, floribus pendulis labello obtuso oris plicatis. *Hall. act. helv.* 4. *p.* 111. Helleborine angustifolia palustris s. pratensis, *Bauh. pin.* 87. *Caulis altior. Spica longa multiflora. Flores fructusque penduli. Flores duplo majores petalis latioribus. Nectarium reliquis petalis cohaerens: cymba lineis purpureis.* H.

grandiflora. 6. S. bulbis fibrosis, fol. ensiformibus, flor. erectis, nectarii labio obtuso petalis breviore. *It. oel.* 144. *Huds. angl.* 341. Serapias bulbis fibrosis, caule paucifloro, flor. distantibus, nectarii labio petalis breviore. *Ger. prov.* 132. Epipactis caule folioso paucifloro, lineis laevibus labelli obtusi. *Hall. act. helv.* 4. *p.* 105. *Flores albi, magni. Fructusque erectus; Labellum breve minus acutum lineis eminentibus.* H.

rubra. 7. S. etc.

Linnaeus accepted four species of Haller's genus *Epipactis*. Haller did not use the binary nomenclature and his names cannot be used.

There are no difficulties with *Serapias rubra* = *Cephalanthera rubra*. We see that Hudson's *Serapias longifolia* is renamed *S. grandiflora* by Linnaeus, but this is not allowed in modern nomenclature and *grandiflora* is a younger synonym and must be rejected for reasons of priority. The right name for the white flowering *Cephalanthera* must be *S. longifolia* Hudson.

The other two species together form the *Serapias latifolia* Hudson, which is divided into two.

Serapias latifolia Hudson is a name which is not legitimate, because, according to art. 63 of modern nomenclature, "when a species is divided into two or more species, the specific epithet must be retained for one of them, or (if it has not been retained) must be reinstated", so that the name had to be *Serapias Helleborine* for our modern genus *Epipactis*. Now this species is divided again: 1) *S. latifolia* and 2) *S. longifolia*. Of course one of these must have the name *S. Helleborine* again.

If we read the diagnoses, we see that in *S. latifolia* Huds. emend. L. the quotation *Fl. suec.* 819 suggests that this diagnosis was already found in the Flora Suecica, but this is not true, for "fol. ovatis amplexicaulibus" is from HALLER. No varieties are distinguished! As to the synonyms it is clear that this species agrees with the Broad-leaved Helleborine (exc. *Cam. epit.*!)

From the diagnosis and the synonyms of *S. longifolia* L. (non Huds.!) we conclude that by this species the Marsh Helleborine is meant, especially from HALLER's diagnosis, which is quoted. Here this name is used for a different plant than the one HUDSON meant and also for a different one than LINNAEUS had in mind in his Spec. Plant. ed. 2, for in this book the plant of Oeland was named *longifolia*. Therefore *S. longifolia* L., 1767, is a younger homonym of *S. longifolia* Huds., 1762, and therefore LINNAEUS' *longifolia* must be rejected.

Three facts prove that LINNAEUS did indeed mean the Marsh Helleborine by his *S. longifolia* (1767):

1) the synonym of HALLER *act. helv.* 4. *p.* 111.
2) LINNAEUS' Mantissa altera (1771) and
3) the sheet of *Serapias* in the herbarium of Hortus Cliffortanus in the British Museum, of which I received a photo by the kindness of Dr. G. Taylor. On this sheet we see in LINNAEUS' handwriting "*Serapias longifolia*" apparently because LINNAEUS revised the sheet and wrote the right name on it (Fig. 2.). This determination cannot have been put on the paper any earlier than 1762, but I suppose in 1767 or later. This determination irrefragibly fixes the epithet *longifolia* L. to the Marsh Helleborine. With this determination the *Serapias longifolia* L. (1767) is typified. However, it will not be possible to use this name in this sense because of its older homonym *S. longifolia* Huds. (1762).

Now Linnaeus divided *Serapias latifolia* Huds. which name should be *Serapias Helleborine* into two species, one of which is *S. longifolia*. L., the Marsh Helleborine, and it will be necessary to reinstate or to retain the name *S. Helleborine* for the rest, the species which is named *S. latifolia* by LINNAEUS and this is the Broad-leaved Helleborine! The most important fact is now that the epithet *Helleborine* can be retained for the species which has had this name the last few years. We see therefore that *Serapias latifolia* Huds. emend. L. must be called *Serapias Helleborine* L. MILLER was the first to use this name in this sense.

In 1768 Philip MILLER published the eighth edition of the Gardeners Dictionary and here four species are distinguished in the genus *Serapias*, the second and the fourth of which, *Serapias Damasonium* and *S. Latifolium*, have white flowers and belong to our *Cephalanthera damasonium*. The first name *S. Helleborine* is used here in a limited sense for the Broad-leaved Helleborine:

> 1. SERAPIAS (*Helleborine*) bulbis fibrosis floribus erectis bractea brevioribus. *Serapias with fibrous bulbs, and erect flowers with short bractea.* Helleborine montana, latifolia C. B. P. 186. *Broad leaved, Mountain, Bastard Hellebore.*

and the description of the flowers runs:

> The stalk is adorned with flowers toward the top, which have some resemblance to those of Orchis: they are composed of two whitish, and three herbaceous petals, which expand; and in the middle appears the nectarium, which has a resemblance of a disboweled body of a fly, of a purplish colour.

The third species is *S. palustre* and this is the Marsh Helleborine, the epithet *palustre* is used by Miller in the same meaning as we do it now:

> SERAPIAS (*Palustre*) bulbis fibrosis. *Serapias with fibrous bulbs, reflexed petals, the lip of the nectarium obtuse, and sword-shaped veined leaves.* Helleborine angustifolia palustris, sive pratensis. C. B. P. 187. *Narrow leaved Marsh, or Meadow Bastard Hellebore.*

and the description of the flowers is:

> .... (The third sort has) faded purplish-coloured flowers, disposed in a loose spike; they have five petals, inclosing a large nectarium like the body of a fly, with a yellowish head striped with purple and a white body; the lip which hangs down, is white and fringed on the edge. This sort flowers in July.

So the species are *Serapias Helleborine* L. emend. Miller and *S. palustre* Miller. The names are validly published and legitimate.

The genus *Serapias* of Linnaeus was not accepted by all the botanists. In 1769 Henrici Ioa. Nepom. Crantz in his Stirpium austriacarum, fasc. VI, publishes *De Orchidum ordine, generibus discursus* and in this work the author uses the binary nomenclature! The genera are quite different from Linnaeus'. We read on p. 462 sub 3:

Epipactis palustris.

> Epipactis caule folioso multifloro, labello articulato vomeriformi, floribus pendulis. Icon. T. I. F. 5.
> Epipactis foliis ensiformibus, floribus pendulis labello obtuso, per oras plicato. HALL. Orch. p. 111. Epipact. 5.
> Helleborine angustifolia palustris. C. B. *pin.* 187.
> Helleborine palustris nostras RAI. Hist. II. certo.
> Helleborine angustifolia RAI. *cantabr.* p. 72?
> Helleborine latifolia, OEDERI Dan. Fasc. V. T. CCLXVII, bona & locus natalis consentit.

The figure is a good one and so is that of Oeder in Flora Danica and there is no doubt that here we have the same epithet as used by Miller for the species Marsh Helleborine, which is validly published and legitimate.

On p. 467 we find Epipactis Helleborine sub no 5:

Epipactis Helleborine.

Epipactis cymba cartilaginea depressa, vernice splendente inuncta; flore minore. F. 6. c.

Epipactis foliis amplexicaulibus ovato-lanceolatis labello lanceolato. HALL. *Orch.* Epip. 4. *non bene.*

With: a) Epipactis rubiginosa etc.
b) Epipactis viridans etc.
c) Epipactis varians etc.

From this it is clear that CRANTZ used the epithet *Helleborine* for the first time in connection with the genus *Epipactis* and so the right name is: *Epipactis Helleborine* (L. em. Mill.) Crantz. The figure given by CRANTZ is the Broad-leaved Helleborine or one of its allies, but only a single flower is depicted. According to JANCHEN a and c are promoted species and so only var. b is now our *E. helleborine.*

In LINNAEUS' last work Mantissa altera he follows HALLER's views and this was easy enough after HALLER's book: Historia Stirpium Helvetiae, vol. II, 1768, in which two beautiful plates are given: tab. 39 *Epipactis foliis ensiformibus*, which is Marsh Helleborine and tab. 40 *Epipactis foliis amplexicaulibus*, which is the Broad-leaved Helleborine. The work had a great influence on LINNAEUS' Mantissa altera: p. 490:

SERAPIAS.

longifolia excludatur tota, substituatur e Syst. nat. 593 integra.
Hall. flor. 1296. t. 39.
Helleborine. *Riv. hex. t.* 3. *Oed. dan. t.* 267.
Petala pubescentia, purpurascentia: interiora 2 alba.
Labium cordatum, obtusum, subserratum e marginatum.
Cymba lineis purpureis et flavis.

latifolia Hall. flor. 1297. t. 40.
Damasonium flore mixto, *Riv. hex. t.* 6.
Helleborine altera, flore atro-rubente. *Bauh. pin.* 187.
Petala pubescentia, virentia: interiora 2 alba.
Labellum cordatum, mucronatum, reflexum.
Cymba lineis nullis.
Obs. S. latifolia et longifolia, rubra et grandiflora differunt quidem, sed minus quam nonnulli exclamarunt.

The capitulation is total! Here LINNAEUS accepts Haller's opinion and he waives his own. But here too *Serapias longifolia* is a later homonym of HUDSON's name and the epithet *longifolia* for the Marsh Helleborine must be rejected. The first name which was legitimate is *Serapias palustre* Miller and the name is now *Epipactis palustris* (Mill.) Crantz. The plate of OEDER's Flora danica sub *Epipactis latifolia*, tab. 267, is mentioned by Crantz as a synonym and this plate can be considered to be the type (Fig. 3) of *Epipactis palustris.*

What is the type of *Serapias Helleborine*? There is no herbarium-specimen from LINNAEUS in the new meaning. But there is a good figure of this species in HALLER's Historia Stirpium Helvetiae, vol. II, tab. 40, and it seems best to choose this as the type (Fig. 4).

SUMMARY

1. *Serapias caule multifolio multifloro* published by LINNAEUS in 1737 is a collective species comprising the species of the genera *Epipactis* and *Cephalanthera* in their modern meaning. The diagnosis is changed in LINNAEUS' later works but his opinion does not change until 1763.

2. In 1753 *Serapias Helleborine* is still the same collective species. LINNAEUS' herbarium specimen, which is determined as *Serapias Helleborine latifolia* is the Marsh Helleborine.

3. Under the influence of the work of HUDSON (1762) LINNAEUS changes his mind and in Species Plantarum ed. 2 (1763) the collective species is divided into *Serapias latifolia* Hudson for the species of the genus *Epipactis* and *S. longifolia* for those of the genus *Cephalanthera* Both species are collective ones.

4. After the publication of HALLER's paper in Act. helv. IV, 1760, in which the binary nomenclature is not yet followed, LINNAEUS in 1767 in Syst. nat. ed. 12 divides *Serapias latifolia* Huds. into two species *Serapias latifolia* Huds. emend. L. for the Broad-leaved Helleborine and *Serapias longifolia* L. for the Marsh Helleborine. The epithet *longifolia*, however, had already been used by HUDSON and therefore *S. longifolia* L. is a later homonym and must be rejected.

5. *Serapias longifolia* Huds. is renamed *S. grandiflora* by LINNAEUS and therefore this name is a later synonym for *S. longifolia* Huds. and for reasons of priority must be rejected. *S. rubra* is now also mentioned.

6. Apparently LINNAEUS revised the herbarium sheet of the Hortus Cliffortianus about 1767 (Syst. nat. ed. 12). This was a Marsh Helleborine and LINNAEUS determines it as *Serapias longifolia* L. This plant can be seen as the type of *S. longifolia* L. (non *S. longifolia* Huds.!) but this name is not legitimate.

7. If a species is divided into two, the original epithet has to be kept or reinstated. Dividing *Serapias Helleborine* L. into two species the epithet had to be kept for *S. latifolia* Huds. In dividing this species again into two, one of the two retains the name *S. Helleborine*.

8. LINNAEUS typifies the Marsh Helleborine with his determination *Serapias longifolia* L. as one part. For the other part, the Broad-leaved Helleborine, the name *S. latifolia* Huds. emend. L. is used but also in this case the eptihet *Helleborine* must be reinstated and so the name is *S. Helleborine* according to current usage. In this sense the name was used by MILLER: *S. Helleborine* L. em. Mill.

9. The oldest legitimate epithet for the Marsh Helleborine is that of MILLER *palustre* (1768) and combined with the genus name *Epipactis* the name for this species has to be *Epipactis palustris* (Mill.) Crantz (1769) and the type for this is the plant depicted in *Flora danica*, tab. 267, because this is given as a synonym by CRANTZ.

10. The oldest legitimate epithet for the Broad-leaved Helleborine is *Helleborine* and the name of the species in the genus *Epipactis* is now *Epipactis Helleborine* (L. em. Mill.) Crantz. The type of the species is the plant depicted by HALLER in *Historia Stirpium Helvetiae*, vol. II, tab. 40.

I am much indebted to Mrs. G. King for her valuable help with the correction of the English translation and to Dr. F. A. Stafleu for his advices.

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MONTIA FONTANA IN NEDERLAND

DOOR

E. W. CLASON

(*Groningen*)

(*received March 23rd, 1955*)

Bij de soort *Montia fontana* L. gaat het om planten met weinig gedifferentieerde vorm, maar met een relatief grote plastiek van de organen. Daarom stuiten de beschrijving en de begrenzing der taxa onder de soort op moeilijkheden. Dit was voor mij aanleiding om een studie te maken van herbariummateriaal van in Nederland gevonden *Montia*-planten en van levende planten uit het Drentse floradistrict (cf. Fig. 8).

Bij de vermelding van de herbariumspecimina heb ik de volgende afkortingen gebruikt:

[AMD] = Hugo de Vries-Laboratorium, Amsterdam.
[GRO] = Herbarium van het Botanisch Laboratorium, Groningen.
[U] = Botanisch Museum en Herbarium, Utrecht.
[L] = Rijksherbarium, Leiden. Hier berust tevens het herbarium van de Koninklijke Nederlandse Botanische Vereniging [NBV], waarop alle vermeldingen betrekking hebben, waarbij de afkortingen AMD, GRO, L of U niet voorkomen.

Aan de Directeuren dezer instellingen zeg ik gaarne dank voor de verleende medewerking. Voorts ben ik veel dank verschuldigd aan Dr S. J. van Ooststroom voor voorlichting op nomenclatorisch gebied en voor critische opmerkingen bij doorlezing van het manuscript.

1. MONTIA-ONDERZOEK IN NEDERLAND

Van Royen (1740) vermeldde de soort, onder de naam *Montia fontana* L., voor het eerst voor Nederland. Zijn Flora Leydensis verscheen drie jaar na de Flora Lapponica, waarin Linnaeus (1737) voor de eerste maal de naam *M. fontana* gebruikte en de soort getypificeerd heeft. In de Species Plantarum verwijst Linnaeus (1753) ook naar Van Royen (1740). Daar Linnaeus in de jaren 1735–1738 in ons land verbleef en ook Leiden bezocht kan m.i. aangenomen worden, dat het onderkennen van de soort in Nederland is geschied onder invloed van Linnaeus. Van eerdere berichten over de soort in Nederland eventueel onder een andere naam heb ik niets kunnen vinden, zie Oudemans (1877, 1882). De Gorter (1781), wiens Flora volgens de uitgave van 1814 „originem suam debet Excursionibus Botanicis, quas Anno 1735 comite Ill. Linnaeo circa Harderovicum feci", geeft een aantal vindplaatsen op zand- en veengronden bij Groningen, in Friesland en bij Zwolle. Als synoniem heeft hij onder andere *Montia aquatica minor* Mich. Het is duidelijk, dat hem (en derhalve ook LINNAEUS) de overblijvende wintergroene planten uit de beken van de Veluwe, onder meer bij Harderwijk, niet bekend zijn geweest.

VAN HALL (1825) is de eerste, die in zijn Flora de beide soorten *M. minor* en *M. rivularis* van GMELIN (1805) in Nederland heeft onderscheiden. Uit zijn tekst is duidelijk, dat hij tot *M. minor* alle kleine planten rekent en tot *M. rivularis* alleen de beekvorm met lange stengels. Dit blijkt nader uit in Herbarium Van Hall bewaard gebleven materiaal van enkele door hem opgegeven vindplaatsen. De planten van Vianen, Heikop, hebben een typische eenjarige habitus, terwijl al het materiaal van de Sijpenberg bij Arnhem verzameld door C. BERGSMA, ongeacht de grootte der planten, de overblijvende habitus hebben.

GMELIN (1805) is de eerste, die de vroeg vergelende planten uit Baden (Duitsland) als een afzonderlijke soort *M. minor* onderscheidde van de overblijvende, wintergroene, eveneens in Baden, in en bij beekjes groeiende planten, die hij tot zijn soort *M. rivularis* rekende.

VAN DEN BOSCH (1850) geeft in de Prodromus ed. 1 van de beide soorten van GMELIN meer vindplaatsen op; van de volgende is het herbariummateriaal nog voorhanden.

M. minor: Amsterdam, V. d. S. Lacoste; Oegstgeest, Molkenboer; Leyderdorp, Van den Bosch; Vianen, Heikop, 1830, Bergsma en Van der Trappen, cf. VAN HALL (1825); Nijmegen, Abeleven. (Sijpenberg staat terecht met vraagteken, zie onder Van Hall; Maastricht volgens LEJEUNE 1827).

M. rivularis: Beekhuizen, V. d. S. Lacoste; Wolfhezen, 1847, Exc. Ned. Bot. Ver., zie Boursse-Wils; Wageningen, Keyenberg, 1833, Wittewaal; Zeelst, Dozy; Putten/Ermelo, Van der Trappen. (Geen herbarium: Maastricht, Meerssensche heide, Van Hoven. Leyden, Molkenboer, staat terecht met een vraagteken aangegeven, zie onder VUYCK (1901).

Het valt op dat V. d. B. geen opgaven heeft uit het Noorden des lands, terwijl de vindplaatsen van D. de Gorter alleen daarvandaan zijn; V. d. B. had toenmaals geen contact met Van Hall (zie WACHTER 1945), zodat van die kant geen vindplaatsen in de Prodromus zijn gekomen. V. d. B. merkt voorts op: „De genoemde planten worden tot de algemeene soort *M. fontana* L. samengetrokken; het zoude zeer wenschelijk zijn na te gaan of we hier ook met door verschillende levensomstandigheden gewijzigde soorten te doen hebben.''

V. D. B. verwijst naar GRENIER et GODRON (1848), die in hun flora van Frankrijk van beide soorten uitvoerige beschrijvingen geven. Bij *M. minor* GMEL. staat onder meer aangegeven: „les cymes terminales munie à leur base d'une bractée scarieuse, ovale, apiculée, opposée à une feuille'' en zaden „fortement tuberculeuses''; bij *M. rivularis* GMEL. onder meer, dat de bloeiwijzen „naissent toujours d'un noeud, pourvu de deux feuilles opposées et égales'' en over de zaden: „chagrinées, plus luisantes''. Het kenmerk van het ongelijke bladpaar onder de eindelingse bloeiwijzen is voor het Nederlandse minor-taxon volgens mijn bevindingen zeer karakteristiek; het is niet zo, dat men dit kenmerk bij alle planten vindt, maar wanneer men een aantal van de meestal dicht opeenstaande planten onderzoekt, zijn er altijd bij die dit onontwikkelde blad hebben. SURINGAR (1873) heeft dit kenmerk reeds in zijn Zakflora (van Nederland) gebruikt.

G. et G. geven bij de synoniemen namen op van WALLROTH (1840), die voor het eerst zaadkenmerken gebruikt om *Montia*-taxa in Westeuropa (Harzgebied) te typeren (zie echter ook VON CHAMISSO 1831). Helaas zijn de beschrijvingen van WALLROTH verward, zodat niet uitgemaakt kan worden, wat hij precies bedoeld heeft.

OUDEMANS (1861) haalt GRENIER et GODRON (1848) aan, maar vermeldt dan resultaten van eigen onderzoek, waarbij hij voor *M. minor* specimina uit de Morsebelse polder bij Leiden en voor *M. rivularis* uit de beekjes achter het Loo en het bos van Wolfheze gebruikte, nog als herbarium aanwezig (zie stuk 3). De taxa verschillen volgens O. ,,hoofdzakelijk door het uiterlijk harer zaden". Hij typeert ze als volgt:

M. minor. Plant dwergachtig. Stengels stijf, rechtopstaande of opstijgende. Bladen bleekgroen. Zaden grofkorrelig en dof van oppervlakte.
M. rivularis. Plant in alle opzichten sterker ontwikkeld. Stengels liggende of dobberende. Bladen donkergroen. Zaden fijnkorrelig en glinsterend van oppervlakte.

O. vermeldt de opgave van G. et G., dat *M. rivularis* overblijvend zou zijn, maar heeft dit blijkbaar niet zelf kunnen verifieren, zodat deze belangrijke eigenschap in zijn typering ontbreekt. In de tweede druk van zijn Flora heeft OUDEMANS (1873) het artikel over *Montia* zeer bekort en wordt bij de zaden van ,,stekelig" gesproken in plaats van ,,korrelig".

VAN EEDEN (1872 resp. 1881) geeft in het grote plaatwerk Flora Batava (1800, laatste deel verschenen in 1930) onder nr 1042 een afbeelding van *M. minor* GMEL. met tekst, naar exemplaren uit de Haarlemmerhout. Van deze vindplaats is veel herbariummateriaal van omstreeks 1870 bewaard gebleven (zie stuk 3). In de beschrijving worden de zaden ,,tuberculato-scabris" genoemd. In de afbeelding zijn de zaden roodbruin gekleurd, blijkbaar heeft de tekenaar onrijp zaad gezien, want de nog aanwezige planten hebben zwart zaad. Vervolgens onder nr 1266 een afbeelding met tekst van *M. rivularis* GMEL. naar een exemplaar uit Wolfheze, Juli 1879, (zie stuk 3). De zaden worden beschreven ,,nitentibus obtuse tuberculato-scabris"; de bladen zouden breder (spatelvormig) zijn dan die van *M. minor*.

VUYCK (1901) heeft in de tweede druk van de Prodromus bij *M. minor* GMEL. een groot aantal vindplaatsen van een groot deel van Nederland opgegeven, waarvan veel herbariummateriaal nog aanwezig is. Bij Oegstgeest staat in een noot de opmerking van Molkenboer en Kerbert, die in stuk 4 (blz. 268) nader aan de orde komt. Bij *M. rivularis* voor het eerst vindplaatsen uit Twente; de planten van Vlieland, S. Boon, moeten naar mijne mening tot *M. minor* gerekend worden.

Nieuw voor Nederland is *M. lamprosperma* CHAM. van de vindplaats Apeldoorn, Wenum, 1899, Kok Ankersmit. Deze determinatie is stellig onjuist, het betreft hier typische *M. rivularis* GMEL. Opmerkelijk is, dat Vuyck de soort niet heeft opgenomen in de door hem bewerkte 13e druk van SURINGAR's Zakflora (1920).

M. lamprosperma is door VON CHAMISSO (1831) gefundeerd op planten, die hij op de Aleoeten verzameld had en die hij karakteriseerde met behulp van het zaad, dat ,,prachtig glanzend met een lichte, fijne nettekening" was, hetgeen hij door een goede tekening verduidelijkt. Ook vermeldt Von Chamisso planten van verschillende vindplaatsen in Noord Europa, die ook glanzende gladde zaden hebben. Ten onrechte meent Von Chamisso, dat *M. minor* en *M. rivularis* volstrekt gelijke zaden hebben, nl. dofzwart, dicht met knobbels bezet; beide soorten beschouwt hij als varieteiten van *M. fontana* L. en zet daarom *M. fontana* L. tegenover zijn *M. lamprosperma*, waardoor veel verwarring is ontstaan.

Koernicke (1863) bericht over *M. lamprosperma* Cham. van Ochta bij St. Petersburg, Rusland (zie Fig. 3 nr 1); het herbariummateriaal in AMD, GRO, en L laat zien, dat dit kleine bleekrossige planten zijn met eindelingse bloeiwijzen, soms met een ongelijk bladpaar en met glad-glinsterend zaad. Ascherson (1872) stelde vast, dat *M. lamprosperma* in de omgeving van Danzig, Westpruisen, voorkwam en daardoor is de soort in de Westeuropese flora's gekomen, naar aanleiding waarvan Vuyck (1901) a.h.w. naar de soort in Nederland zal hebben ,,uitgezien".

Kloos (1937) geeft een aantekening over *M. lamprosperma* Cham. Na een opmerking over de verwarde nomenclatuur, zegt hij, dat *M. lamprosperma* in kenmerken vrijwel tussen *M. minor* en *M. rivularis* in staat. *M. minor* en *M. lamprosperma* komen volgens hem overeen, behalve wat de zaden betreft, die bij *M. rivularis* en *M. lamprosperma* glimmend en bij *M. minor* dof zijn. Kloos lijkt het verschil in zaad weinig sprekend, hij meent dat er alleen verschil in kleur is, nl. bij *M. minor* iets blauwachtig zwart en bij de andere beide soorten bruinachtig zwart. Deze bevindingen kan ik niet bevestigen; de determinaties van Kloos voorkomende op het materiaal in L. kan ik merendeels niet onderschrijven. Toch komt Kloos de eer toe het eerst over *M. lamprosperma* gevonden in Nederland gepubliceerd te hebben, want de door hem vermelde planten van Ootmarsum 1934, verzameld door J. Heimans, met glinsterende, gladde zaden, moeten ongetwijfeld tot dit taxon gerekend worden.

Clason (1953) beschrijft voor het eerst planten van een vindplaats van *M. rivularis* in Noord-Drente en wel de landvorm onder de naam *M. rivularis* var. *lamprosperma* Beck (1896) non Cham.

Samenvatting. Het *Montia*-onderzoek in Nederland heeft drie taxa opgeleverd. Er bestaat onzekerheid, omtrent hoe zij verschillen, hoe zij gescheiden bestaan blijven, of de verschillen al of niet erfelijk zijn, kortom: over de aard van deze taxa. In nauw verband hiermede staat de nomenclatuur, die ook getoetst dient te worden aan de nieuwste inzichten dienaangaande in het buitenland, cf. Walters (1953), rekening houdende met de internationale nomenclatuurregels.

2. Nomenclatuur

De bij het Montia-onderzoek in Nederland voor de dag gekomen taxa betreffen:

1. eenjarige planten met glinsterend, glad zaad;
2. eenjarige planten met dof, geknobbeld zaad;
3. overblijvende, wintergroene planten met glanzend en althans op de rugkant geknobbeld zaad.

Deze drie taxa verschillen naar mijne mening niet voldoende om ze de rang van afzonderlijke soorten te geven. Voorts zie ik een meer principieel verschil tussen taxon 1 en 2 ten opzichte van 3, dan er tussen

1 en 2 onderling aanwezig is. Daarom meen ik de verhouding tussen de drie taxa te moeten weergeven door taxon 3 de rang van subspecies toe te kennen, terwijl 1 en 2 met de rang van varieteit samen een subspecies vormen. In de volgende stukken wordt dit nog nader gemotiveerd, doch het komt mij gewenst voor eerst na te gaan, wat de wettige namen voor deze taxa in de boven aangegeven rang zijn volgens de internationale nomenclatuurcode, teneinde die namen in de volgende stukken te kunnen gebruiken.

Het Nomenclatorisch type van Montia fontana L.

De soortsnaam *Montia fontana* heeft Linnaeus (1737) voor het eerst gebruikt in de Flora Lapponica en aangehouden in zijn Species Plantarum (1753). In laatstgenoemd werk verwijst Linnaeus, behalve naar de Flora Lapponica, ook naar zijn Flora Suecica (1745) en naar Van Royen (1740), doch deze beide werken verwijzen zonder toevoegingen eveneens naar de Flora Lapponica.

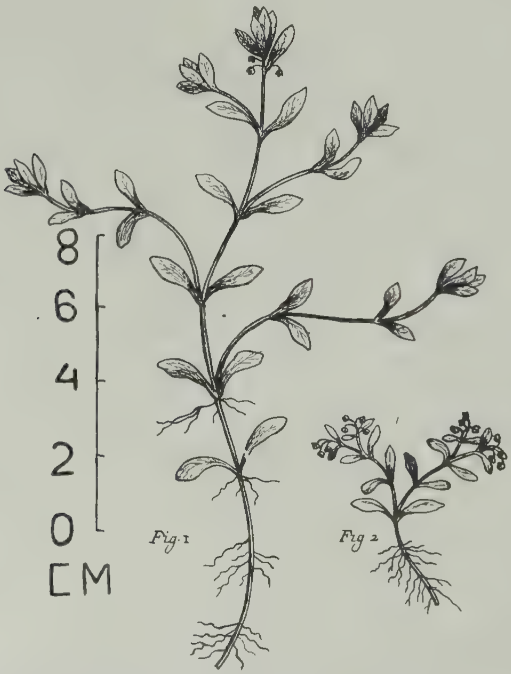

Fig. 1. De afbeelding van Michelius (1729), waarheen Linnaeus (1737) in de Flora Lapponica verwijst.

De Flora Lapponica moet derhalve uitsluitsel geven over wat Linnaeus als type van zijn soort in 1753 voor ogen heeft gestaan. L.

laat zich daar in obs. β, p. 99, als volgt uit: „De zegslieden stellen een tweede soort op, ik echter heb (slechts) een enkele soort gezien, die op wonderbaarlijke wijze „speelt" wat de grootte betreft. Indien echter die andere soort bloemen draagt in de „vleugels", zoals deze (mijn) soort opvallend voortbrengt aan de top, evenals de hooggeleerde Michelius afbeeldt, dan is de soort verschillend, anders niet." Het blijkt hier zonneklaar (zie ook Fig. 1), dat de planten die LINNAEUS in Lapland kende, opvallende, eindelings geplaatste bloeiwijzen aan de top van de stengels droegen, waarmee zich het teken voor eenjarig in zijn Flora Lapponica laat verenigen.

LINNAEUS (1737 en 1753) heeft geen zaadkenmerken gebruikt om zijn soort te typeren. Aangezien volgens LINDMAN (1915) en HYLANDER (1945) in Zweden en noordelijker alleen planten voorkomen met een gladde zaadhuid en derhalve LINNAEUS in de Flora Lapponica alleen dergelijke planten bedoeld kan hebben, waarop LINDMAN en HYLANDER reeds gewezen hebben, kan ik mij er mee verenigen, dat aangenomen wordt, dat het type deze zaden heeft. Dit is ook gedaan door RYDBERG (1932) en WALTERS (1953). Uit WALTERS valt op te maken, dat de plant, die zich onder de naam *M. fontana* in het herbarium van LINNAEUS te Londen bevindt, overeenkomt met het type van de Flora Lapponica en gladde zaden heeft, want WALTERS noemt deze plant als het type-exemplaar van de soort. *M. lamprosperma* CHAM. (1831) is een latere naam voor *M. fontana* L. s.s.

De wettige naam voor de Nederlandse varieteit met glinsterend, glad zaad is derhalve **Montia fontana** L. ssp. **fontana** var. **fontana**.

DE PLANTEN MET DOF, GEKNOBBELD ZAAD

De vraag rijst of de eenjarige *Montia*-planten met dof, geknobbeld zaad tot de soort *M. fontana* L. behoren te worden gerekend. LINNAUES (1753) heeft dat ongetwijfeld gedaan, zoals blijkt uit de platen van de auteurs, waarheen hij bij de synoniemen verwijst, met name Michelius, Dillenius, Vaillant en Van Royen.

MICHELIUS (1729) geeft op zijn plaat 13 twee zeer duidelijke afbeeldingen (Fig. 1). Zijn figuur 2 is van een plant onder de naam van *Montia aquatica minor* met opvallende eindelingse bloeiwijzen, waarbij aan de stijf en vorksgewijze vertakte stengel tussen het bebladerde gedeelte geen wortels zitten. Het mede afgebeelde zaad is weergegeven met rijen stippen gescheiden door strepen en zonder glimlicht, d.w.z. dof en geknobbeld.

DILLENIUS (1719) beeldt onder de naam *Cameraria arvensis et minor* op zijn plaat VI een plant af uit de omgeving van Giessen (Duitsland). Aan de top van de stengel komen uit twee klein gebleven bladeren twee bloemen te voorschijn. Het zaad is afgebeeld met streepjes zonder glimlicht, dus dof.

VAILLANT (1727) geeft onder de naam *Alsinoides annua verna* op zijn plaat 3, fig. 4 een zeer duidelijke tekening van een *Montia* uit de omgeving van Parijs. Alleen de liggende stengeltjes onderaan dragen wortels, de bloeiwijzen zijn eindelings (op één plaats is een ongelijk bladpaar) en het zaad is gestreept getekend.

De verwijzing naar VAN ROYEN (1740) kan alleen maar betrekking hebben op planten met dof, geknobbeld zaad, die bij Leiden meermalen gevonden zijn, terwijl planten met glinsterend, glad zaad vandaar niet bekend zijn.

De eerste, die dit taxon een wettige naam heeft gegeven in de rang van varieteit, is FENZL (1844–46), die, in het toenmalige russische imperium, waartoe ook de Aleoeten (type-vindplaats van *M. lamprosperma* CHAM.) behoorden, van *M. fontana* L. twee varieteiten onderscheidde, nl. *α chondrosperma* met dikgeknobbelde, doffe zaden, naast *β lamprosperma* (syn. *M. lamprosperma* CHAM.).

De wettige naam voor ons taxon is derhalve **Montia fontana** L. ssp. **fontana** var. **chondrosperma** FENZL.

De eerste, die het taxon een geldige naam heeft gegeven, is GMELIN (1805) in de rang van soort *M. minor.* Weliswaar noemt G. geen zaadkenmerken, maar uit ASCHERSON (1872) blijkt, dat de planten van Gmelin dof zaad hadden, terwijl *Montia* met gladde, glinsterende zaden in Baden niet gevonden werd. *M. verna* NECK. (1768) is volgens WALTERS (1953) een ,,nomen illeg., quoad descr.'' PERSOON (1805) heeft een varieteit *β erecta,* doch het is uit de beschrijving ,,caule erecto fol. lanceolatis'' niet uit te maken of daarmee het onderhavige taxon bedoeld wordt.

DE OVERBLIJVENDE, WINTERGROENE PLANTEN MET GLANZEND EN ALTHANS AAN DE RUGKANT GEKNOBBELD ZAAD

LINNAEUS (1737 en 1753) heeft zijn soort *M. fontana* uitdrukkelijk beperkt tot eenjarige planten met eindelingse bloeiwijzen, terwijl de door MICHELIUS (1729) afgebeelde plant uit Bohemen (zijn fig. 2 in mijn Fig. 1) met zijdelingse bloeiwijze en goed ontwikkelde topbladeren volgens hem tot een andere soort gebracht moest worden. Het is merkwaardig dat deze door LINNAEUS (1737) reeds voorziene soort eerst door GMELIN (1805) onder de naam *M. rivularis* inderdaad beschreven werd. Na lezing van wat GMELIN (1805) over deze soort schrijft, twijfel ik er niet aan, dat de Nederlandse overblijvende planten overeenkomen met zijn Badense. Er is m.i. geen reden om met WALTERS (1953) aan te nemen, dat wegens het verloren gaan van het herbarium van GMELIN in Karlsruhe in de laatste oorlog niet meer uitgemaakt kan worden, wat met *M. rivularis* bedoeld wordt. Toegegeven moet worden, dat orgaankenmerken door GMELIN slechts beknopt opgegeven werden en ook, dat deze wat betreft het minder vergroeid zijn der bladbases bij *M. rivularis* ten opzichte van *M. minor,* niet of niet altijd opgaan. De soort wordt door GMELIN het beste gekarakteriseerd als wintergroen, ten opzichte van eenjarig met vroege vergeling bij *Montia minor,* en als groeiende met lange, zwevende stengels in beekjes. Voorts hebben wij het getuigenis van ASCHERSON (1872) over de Badense planten, zie ook ASCHERSON und GRAEBNER (1915). Door de nauwkeurige vindplaatsopgaven van GMELIN (1805) zal het gemakkelijk zijn een topotype van de soort te verzamelen. Hoewel GMELIN geen zaadkenmerken heeft gebruikt, staat het m.i. vast welke planten deze tot zijn soort gerekend heeft.

Indien vergeleken worden planten van de ssp. *fontana* var. *chondrosperma* FENZL (syn. *M. minor* GMEL.) van vochtig zand met planten van *M. rivularis* uit een beek, dan zal men ongetwijfeld tot twee taxa met de rang van soort besluiten. Het is echter zo, dat b.v. de eenjarige *chondrosperma*-planten van natte veengrond en de landvorm van *M. rivularis*, althans oppervlakkig, een zodanige overeenkomst kunnen vertonen, dat ik er de voorkeur aan geef alle Nederlandse planten tot één soort te brengen, die dan *Montia fontana* L. moet heten.

De overblijvende, wintergroene planten met althans aan de rugkant geknobbelde zaden reken ik tot een afzonderlijke subspecies (naast ssp. *fontana*). De wettige naam hiervan is **Montia fontana** L. ssp. **rivularis** (GMELIN) SCHUEBLER ET MARTENS (1834). S. en M. hebben voor het eerst de naam *rivularis* van GMELIN (1805) gebruikt in de rang van subspecies onder de soort *Montia fontana* L.

3. TAXONOMIE

Montia fontana L.

M. fontana L. (1753). Sp. Pl. 87.
Eumontia PAX et K. HOFFMAN (1934). In: ENGLER und PRANTL, Nat. Pflz. Fam. Ed. 2; 16c: 234–262.

Eenjarige of overblijvende-wintergroene *Montia*-planten met vezelige wortels. Bloemkroon vijfslippig, met korte buis die aan een zijde door een spleet open is en met drie korte en twee iets langere kroonslippen.

Subsp. **fontana**.

M. fontana L. (1953). Sp. Pl. 87, sensu stricto.

Stengels min of meer gevorkt vertakt, stijf rechtop of opstijgend, tot 10 cm lang. Wortels onderaan de stengel in de grond en niet aan de bovengrondse delen. Bloeiwijze opvallend eindelings of ook in de oksels der lager geplaatste stengelbladen, bij vruchtrijpheid dikwijls groot ten opzichte van de rest van de plant. Eenjarig, bloei in April/Mei en dikwijls reeds vergeeld voor het geheel uitrijpen der zaden in Juni/Juli.

var. **fontana**.

M. fontana L. (1753). Sp. Pl. 87, sensu stricto.
M. lamprosperma CHAMISSO (1831). Linnaea 6 : 564.
M. fontana L. ssp. *fontana*. WALTERS (1953). Watsonia 3 : 2.

Zaden met dunne, gemakkelijk scheurende zaadhuid, die ook met het blote oog gezien glinstert en nergens knobbels vertoont. Type: De planten door LINNAEUS (1737) gevonden in Lapland, subsidiair de plant in het herbarium van Linnaeus in Londen, volgens WALTERS (1953).

OECOLOGIE

Tot nu toe alleen gevonden in Twente, ten Noorden van Enschedé, provincie Overijsel, zie herbariummateriaal, alsmede in De Lutte ten Oosten van Oldenzaal, volgens ZWART (1950). Bij Hezinge onder Vasse zijn de planten in het voorjaar zodevormend in een elzenbosje in het brongebied van de Mosbeek. Op 6–6–1954 noteerde ik op deze groeiplaats onder de elzen: *Equisetum palustre* L. (zeer veel), *Solanum dulcamara* L. (veel), *Phragmites communis* TRIN., *Valeriana officinalis* L., *Angelica sylvestris* L., *Stellaria alsine* GRIMM. (zeer veel op lichte plekken), *Cirsium palustre* (L.) SCOP., *Eupatorium cannabinum* L., *Polygonum mite* SCHRANK., *Urtica dioica* L. en *Epilobium palustre* L.; op 31–10–1954 was het aspect belangrijk veranderd door het ontbreken van de *Montia*, *Equisetum palustre* L. en de grote bloeiende planten, door de aanwezigheid van veel dood blad van *Alnus glutinosa* GAERTN., terwijl *Stellaria alsine* GRIMM zo mogelijk nog meer voorkwam dan in de voorzomer. De grond van het elzenbosje bestaat uit een 20 tot 40

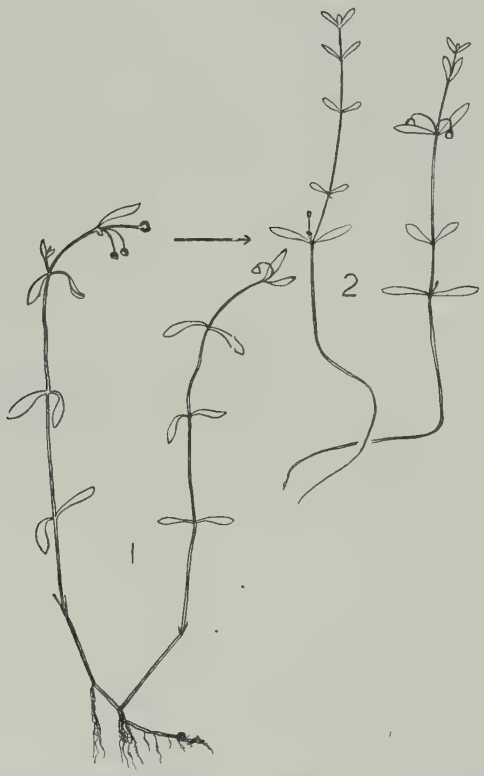

Fig. 2. *Montia fontana* L. ssp. *fontana* var. *fontana*: 1. van de Mosbeek, 6–6–1954, E. W. Clason. 2. idem, na tot 3–7–1954 te zijn doorgegroeid (zie tekst)

cm dikke laag doornatte vergane plantendelen op blijkbaar ondoorlatende leemondergrond. Langs de Mosbeek en de beken in het naburige Sprengendal komt deze varieteit ook voor op brongronden buiten het elzenbos en dan samen met de subspecies *rivularis*.

HERBARIUMMATERIAAL VAN NEDERLAND

Prov. Overijsel, Twente: Lonneker, Penningskotten, 21–6–1905, M. J. Blijdenstein (*M. minor*). Ootmarsum, Sprengendal, 25–7–1934, J. Heimans, h. pr.; 3–8–1946, S. J. van Ooststroom nr 8443, [L]; 3–8–1946, J. Heimans, h. pr. Vasse, bronnen, 3–8–1946, Joh. Jansen (*M. fontana* L. ssp. *rivularis* Oborny [1]; brongebied van de Mosbeek, 17–6–1948, Gron. Biol. Club, [GRO]; id., vegetatievormend onder Elzenbroekbos, 6–6–1954, E. W. Clason, [AMD, L, GRO] (Fig. 2).

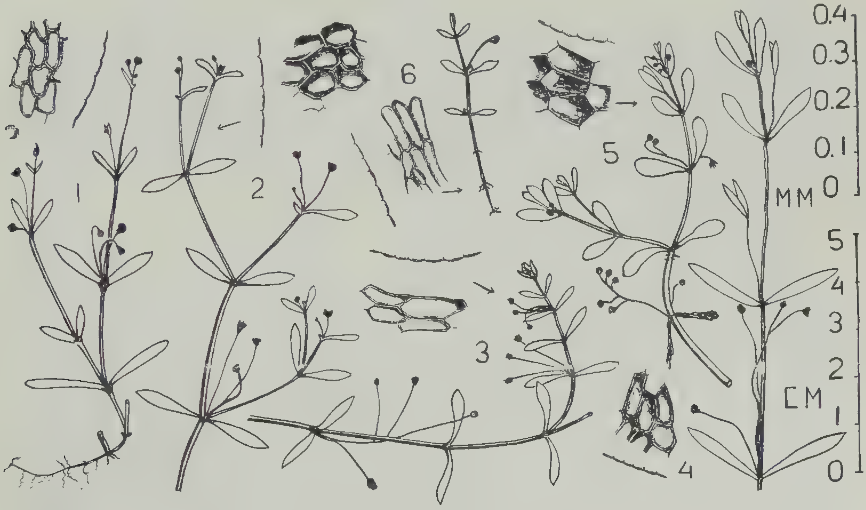

Fig. 3. *Montia fontana* L. met glad, glinsterend zaad van buiten Nederland: 1. St. Petersburg, Ochta, 6–1857, Koernicke, [L]. 2. Finland, Lapponia Kemensis, 9–1909, J. Montell, [L]. 3. Zweden, Blecingik, 28–6–1912, J. Erickson, [AMD]. 4. Moravia, Dittersdorf, 7–1931, A. Laus, [L]. 5. N. Amerika, Washington, 7–1899, W. N. Suksdorf, [L]. 6. Ned. Nieuw Guinea, Wilhelminatop, 9–1938, L. J. Brass & E. Meyer Drees, [L].

VOORKOMEM BUITEN NEDERLAND

Aan de hand van de literatuur (cf. Von Poellnitz 1942) en materiaal in de Nederlandse herbaria vormde ik mij het volgende, voorlopige beeld van de verspreiding: Aljaska. Canada. N. Amerika (zie Fig. 3 nr 5). Groenland. IJsland. Lapland. Finland (zie Fig. 3 nr 2). Zweden (zie Fig. 3 nr 3). Rusland (zie Fig. 3 nr 1). ? N. Azië tot Japan. Oost-Duitsland. Zwitserland. Oostenrijk. Bohemen. Moravië (zie Fig. 3 nr 4). Spanje. N. Engeland. Ierland. Kenya. Z. Amerika. Zuidelijke gematigde Oceanische Eilanden. Nieuw Zeeland. Nederlands Nieuw

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[1] Oborny (1885–1890) heeft alleen de soorten van Gmelin (1805).

Guinea (zie Fig. 3 nr 6). De verspreiding schijnt in hoofdzaak subarctisch, boreaal en alpien te zijn. Het verspreidingsgebied in Nederland bij Ootmarsum is daardoor wel merkwaardig; dat de soort in het aangrenzende deel van Duitsland voorkomt is mij niet bekend, doch uiteraard wel te verwachten.

var. **chondrosperma** FENZL (1844). In: LEDEBOUR, Fl. Rossican 2:152.

M. fontana L. (1753). Sp. Pl. 87, pro parte.
M. verna NECKER (1768). Delic. Fl. Gallo-Belg. 1 : 78.
M. minor C. C. GMELIN (1805). Fl. Bad. Als. 1 : 301.
M. fontana L. ssp. *chondrosperma* (FENZL) WALTERS (1953). Watsonia 3 : 2.

Zaden met het blote oog gezien dof, aan alle kanten bezet met meer of minder duidelijke knobbeltjes. Type: De planten uit Baden beschreven door GMELIN (1805). Volgens WALTERS (1953) is het typemateriaal van Gmelin in Karlsruhe in de laatste oorlog verloren gegaan; het is wenselijk, dat op de nauwkeurig omschreven vindplaatsen van Gmelin een topo-type wordt verzameld.

OECOLOGIE

In alle floradistricten van Nederland op vochtige zand-, leem- en veengronden. Dikwijls zodevormend op onbegroeide aarde, zoals slootranden en opgebaggerde slootgrond, in grote aantallen tussen grassen (ook rogge), eveneens tussen mossen. Zonnige tot lichtbeschaduwde plaatsen. Het ondervolgend opgegeven herbariummateriaal geeft geen goed beeld van de verspreiding in Nederland, daar niet overal even intensief gezocht is. Tot nu toe zijn er geen opgaven van vindplaatsen op kleigronden. De planten hebben slechts een gering concurrentievermogen, waardoor ze blijkbaar vooral deel uit maken van pionierbegroeiingen.

HERBARIUMMATERIAAL VAN NEDERLAND

WADDENDUINDISTRICT: Ameland, tussen Nes en Buren, 29–4–1869, F. Holkema (Fig. 4 nr 5); Hollum, 25–5–1896, L. Vuyck. Terschelling, Lieser Plak, 10–5–1896, F. Holkema; Midsland, elzenbosje, 1897, L. Vuyck. Vlieland, 5–7–1898, S. Boon. Texel, 6–1890, H. W. Groll.
DUINDISTRICT: Haarlem, Bronstee, F. L. Splitgerber (*M. fontana* L. var. *a*). Haarlemmerhout, 18–5–1841, herb. Kerbert; id. tussen vochtig mos, 16–5–1831, C. A. J. A. Oudemans nr 683 (Fig. 4 nr 6) [AMD, GRO, L]; id., 28–4–1869 en 5–1868, F. W. van Eeden; Ogterop, [L]. Noordwijkerhout, houtbosje op het Langeveld, 15–5–1836, Schuurmans Stekhoven. Wassenaar, Zuidwijk, 11–6–1941, Lam c.s. [L]; buiten Prins Frederik, tussen kreupelhout, 5–1873, Boerlage. Den Haag, Huis ten Bosch, 15–5–1899, W. J. Jongmans, [L]; 14–5–1898, P. J. van Breemen, [L]. Haagse Bos, 30–4–1896, C. M. L. Popta, [L]; langs de vijver, 15–5–1899, Vuyck; op een grasveld, 5–1909, [L]. 'sGravenzande, 26–5–1901, P. J. van Breemen & F. K. van Iterson, [L]. Monster, 21–5–1905, P. Jansen & W. H. Wachter; 18–5–1900, J. F. Wichard. Domburg, manteling van Duinvliet, 5–1877, D. Lako, [L] (Fig. 4 nr 3). Oost Kapelle, zandig bouwland, 5–1877, D. Lako.
OOSTELIJK HAFDISTRICT: geen materiaal. Joure en Langweer, op een zandstrook, zie onder Drents District.

Westelijk Hafdistrict: Amsterdam, op veengrond bij den Voetangel, 7–1845 en venen bij Nieuweramstel, 9–1906, J. S. v. d. Sande Lacoste; Vondelpark, 12–5–1901, Ogterop, [L]. Utrecht, Willinkpark in grasveld, 5–1906, W. C. van Embden [L]., Oegstgeest, vochtig weiland, 3–1836, J. S. v. d. Sande Lacoste; in de Morsebelse polder, 7–5–1836, J. Schuurmans Stekhoven; langs sloten, Molkenboer en idem, Boursse Wils; weilanden, Kerbert & Molkenboer (Fig. 12 nr 1). Leiden, polder, herb. Kerbert; Dozy; op vochtige, beschaduwde zandgrond, ?Molkenboer; Duivenvoorde, 27–5–1946, De Jongh, De Leeuw & Wachter, [L]. Warmond, vochtige zandgrond, 22–4–1874; Biol. stud. Leiden.

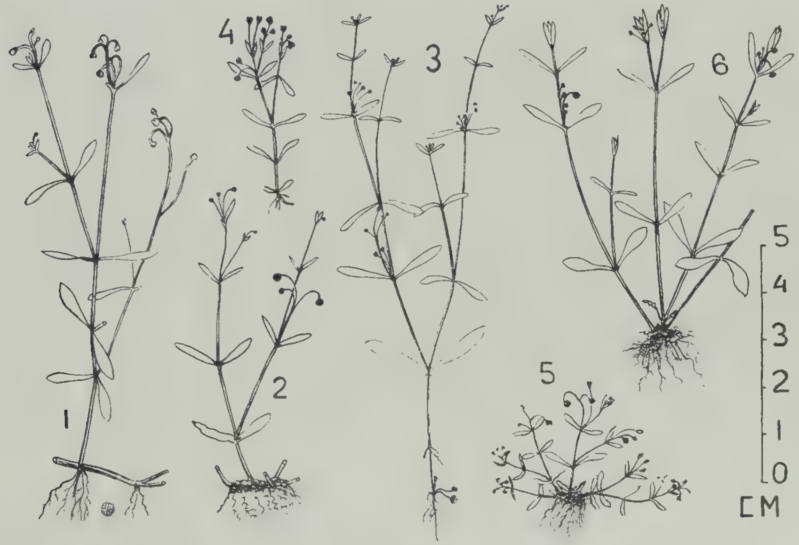

Fig. 4. *Montia fontana* L. ssp. *fontana* var. *chondrosperma* Fenzl.: 1. Natte veengrond, Onnen, 20–5–1953, E. W. Clason. 2. Tuingrond, Baarn, 26–5–1929, S. J. van Ooststroom. 3. Manteling, Domburg, 5–1877, D. Lako. 4. Vochtige zandgrond, Haren, 30–5–1933, P. Buwalda. 5. Zandgrond, Ameland, 29–4–1869, F. Holkema. 6. Vochtig mos, Haarlemmerhout, 16–5–1871, C. A. J. A. Oudemans.

Fluviatiel District: Vianen, Heikop, 1824, Bergsma, [GRO]; 1830, Bergsma & Van der Trappen; Bergsma, [U]. Gorkum, don, bij Noordeloos, 26–5–1925, C. G. G. J. van Steenis. Utrecht, slootkant, Ruigenhoekse dijk, 5–1913, W. C. van Embden, [L]. Jutfaas, Liesbos, 3–6–1897, D. Bolten, [L]. Zeeuws Vlaanderen, Sas van Gent, 9–6–1855 en Axel 4–1859, A. Walraven, [NBV, L]. Zwolle, Vecht, Berkum, op vochtige zandgrond, 5–1900, D. Lako, [L].

Drents District: bij Groningen, J. Wittewaal (Fig. 4), [U]. *Noord Drente*: Eelderwolde, Cayaux; herb. Dassen; 5–5–1869, H. C. van Hall; straatweg, 21–4–1868, F. Holkema; 20–5–1906, R. de Boer & H. Kooi, [GRO]. Paterswolde, 3–5–1831, [U]. Slochteren, Schaaphok, 17–6–1841, Th. Sprée. Haren, 6–1856, Stratingh, [GRO]. N. W. vaart, vochtige zandgrond, 31–5–1933, P. Buwalda (Fig. 4 nr 4), [GRO]. Sassenhein, 4–5–1935, L. K. Wiersum, [GRO]; Onnen, natte veengrond, 12–5–1953, E. W. Clason (Fig. 4 nr 1), [GRO]. Glimmen, wegkant, 2–5–1906, H. Burger, [GRO]. Peize, C. de Gavere; 5–6–1857, Stratingh, [GRO]. *Westerwolde*: Wedde, burcht, 6–1889, W. W. Schipper, [GRO]. *Friese Wouden*: Oldeberkoop, H. Albarda. Tussen Joure en Langweer, 5–1887, C. Brakman, [L]. *Coevorden*: Weyerswoud, langs de weg, 20–5–1902, Goethart & Jongmans, [L]. Dalen, slootkanten in

de Ma, 6–1946, J. Kern nr 5543, [L]. *Noord-Twente*: Ootmarsum, op vochtige open zandgrond, 5–1896, D. Lako, [L].
GELDERS DISTRICT: *Overijsel*: Dalfsen, slootkant langs de Dommeler dijk, 5–1905, D. Lako, [L]. Daarle, 17-5–1902, Goethart, Jongmans & Lako, [L]. *Veluwe-Utr. Heuvelrug*: Harderwijk, 7–1864, en Hierdermeent, 6–1877, R. Bondam. Nijkerk, zandweg bij Slichtenhorst, 6–1904, F. A. des Tombe, [L]. Apeldoorn, bij Teuge, onder rogge, 21–5–1875, en bouwland aan het oude kerkpad, 4–1877, Kok Ankersmit, [L]; de Kar, J. Koorneef; bouwland, 27–4–1878, J. D. Kobus. Scherpenzeel, vochtige zandgrond tussen het koren, resp. in greppels, 22–4–1820, C. G. G. J. van Steenis, [U]. Amersfoort, C. A. Bergsma. Driebergen, boomkwekerij, herb. Coster. Woudenberg, tussen koren, 22–5–1920, C. G. G. J. van Steenis. Zeist, Pyramide, zandterrein, 11–5–1924, C. G. G. J. van Steenis. De Bilt, 1902, [U]. Stoutenburg, vochtige zandgrond, 3–5–1893, Garjeanne. Bennekom, 28–4–1948, F. A. Stafleu, [U]. Lunteren, op bouwland, 5–5–1902, Goethart & Jongmans. Veenendaal, in een roggeveld, Goethart & Jongmans, [L]. Barneveld, vochtige zandgrond, F. A. des Tombe, [L]. *Gooi*: Bussum, boomkwekerij, 11–5–1919, B. H. Danser, [GRO]. Hilversum, Meent, 13–5–1899, Th. Weevers. Baarn, 3–6–1919, H. Uittien, [U]; id., tuin Lab. W. C. Scholten, Javalaan, 26–5–1929, S. J. van Ooststroom nr 2119, [L] (Fig. 4 nr. 2). Huizer Meent, 5–1909, W. J. C. Kooper, [U].
SUBCENTREUROOP DISTRICT: *Twente*: Markelo, op bouwland, 19–5–1898, Goethart & Vuyck. Lonneker, langs de weg van Espelo naar Enschede, 5–1901, D. Lako, [L]. Enschede, vochtige zandgrond in tuin, 4–1906, M. J. Blijdenstein (Fig. 12 nr 2 & 3). Ruurlo, onder eiken bij Elschot, 5–1895, J. Ensink A. Jzn., [AMD, NBV]. *Nijmegen*: Wychense venen, N. Abeleven; Haterse broek, M. Coenen. Overasselt, roggevelden, 5–6–1897, Goethart & Vuyck. Noord-Limburg; Ottersum, roggeland bij het Koningsveen, 7–6–1897, Goethart & Vuyck.
KEMPENS DISTRICT: Oorschot, vochtige zandgrond, 7–1839, De Bruyn. Vughtse Heide, 4–1848, F. van Hoven. De Peel, zandgrond, 2–6–1873, De Vries. Breda, vochtige roggelanden, 3–6–1897, L. Vuyck.
LÖSSDISTRICT PROV. LIMBURG: Schinnen, in bouwland, 4–1869, J. S. v. d. Sande Lacoste. Schinveld, heidesloot nabij het moeras van de Rode Beek, 27–5–1901, Goethart & Vuyck, [L]. Brunssum, veen, 5–1911, A. de Wever.

VOORKOMEN BUITEN NEDERLAND

Aan de hand van literatuur en materiaal in de Nederlandse herbaria vormde ik mij het volgende, voorlopige beeld van de verspreiding. Zuid-Zweden. Oost-Duitsland, zie Fig. 5 nr 1. West Duitsland, zie Fig. 5 nr 2. Zwitserland. Frankrijk. Zuid- en Midden-Engeland. Ierland. Noord-Amerika. ?Centraal Azië. ?Australië.

Subsp. **rivularis** (GMELIN) SCHUEBLER et MARTENS (1834). Fl. v. Würtemberg, 88.

Montia fontana L. subspecies *intermedia* (BEEBY) WALTERS (1953). Watsonia 3 : 5.

?Montia fontana L. subspecies *variabilis* WALTERS (1953). Watsonia 3 :5.
Stengels slap; vertakt; ook boven de grond en aan het bebladerd gedeelte dikwijls met wortels. Bloeiwijzen in de bladoksels; die aan de top zijn niet of nauwelijks langer dan de topbladeren. Laatste bladparen aan de top steeds bestaande uit gelijke grote bladeren, groen, dikwijls opvallend groot. Zaden met het blote oog gezien glanzend, althans aan de rugzijde met duidelijke, dikwijls scherpe knobbeltjes. Overblijvend-wintergroen, bloei van April tot September.
Type: De planten uit Baden beschreven door GMELIN (1805). Voorts zelfde opmerking als bij de var. *chondrosperma*.

forma **rivularis**.

M. rivularis C. C. GMELIN (1805). Fl. Bad. Als. 1 : 302.

Stengels in het water zwevend, tot 60 cm lang, slechts de bebladerde toppen dobberend aan de oppervlakte van het water.

forma **terrestre** nov.

M. rivularis GMELIN var. *lamprosperma* BECK (non CHAM.) (1896). Fl. Nieder-Oestr. 1 : 385.

M. limosa DECKER (1927). Verh. Bot. Ver. Brandenburg 69 : 57.

Stengels los kussenvormig tegen elkaar opgroeiend buiten het water, met luchtwortels, tot 10 cm lang.

De beide vormen zijn niet scherp gescheiden en phaenotypisch. In de ondervolgende opgaven worden zij niet uit elkaar gehouden.

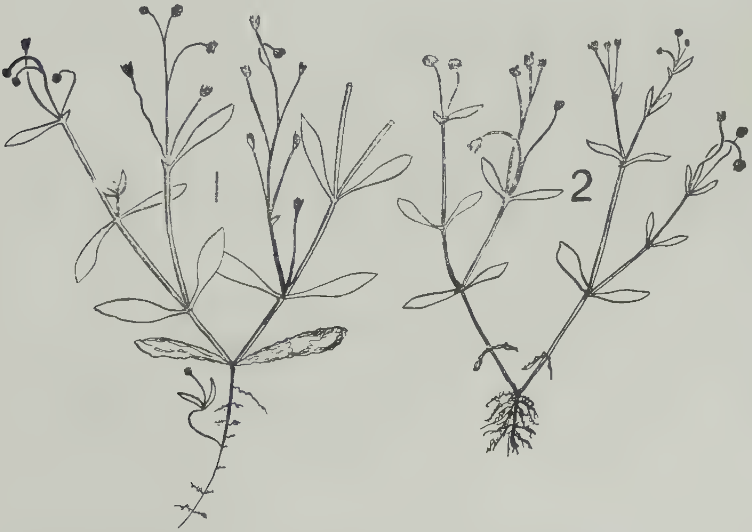

Fig. 5. *Montia fontana* L. ssp. *fontana* var. *chondrosperma* FENZL: 1. Pommern, Greifswald, 17–6–1881, Ross, [AMD]. 2. Westfalen, Wattenscheid, Schemann, [AMD]. Nat. gr.

OECOLOGIE

De watervorm (f. *rivularis*) komt voor in beekjes met helder water. Bij transplantatieproeven in het natuurterrein van Hortus De Wolf (Haren bij Groningen) bleek in stilstaand water deze Montia niet te kunnen concurreren met groene draadwieren. De landvorm (f. *terrestre*) komt voor in beekdalen, op brongronden en moerasveen, aan greppelranden in weiland, in vers gegraven greppels en slootjes op natte leemgronden. Deze standplaatsen komen voor in het Gelders, Drents, Subcentreuroop en Kempens floradistrict van Nederland, zodat de vindplaatsen daar worden aangetroffen (Fig. 8).

De planten hebben weinig concurrentievermogen en krijgen hun ontwikkelingskansen op plaatsen, waar het plantendek geregeld vernield wordt. In beekjes is dit laatste een natuurlijke omstandigheid, in de andere gevallen meest het gevolg van bodemcultuur door de mens. De landvorm komt dikwijls voor in greppels in beekdalen naast *Philonotis fontana* (L.) Brid. en *Cardamine amara* L., terwijl *Chrysosplenium* spec. ook vaak in de buurt groeit. Drude (1902) schrijft reeds, dat *Montia fontana rivularis* met *Stellaria alsine* Grimm hoog in de Alpen kleine bronmoerassen geheel kunnen opvullen. Schroeter (1926) geeft van deze bronmoerasjes een levendige beschrijving en noemt als typische „Quelle und Quellbach bewohnende Blütenpflanze" ook *Cardamine amara* L., — naast *Arabis bellidifolia* Jacq., *Saxifraga stellaris* L., *S. aizoides* L., *Sedum villosum* L., *Epilobium alsinifolium* Vill., *E. alpinum* L., en *E. nutans* Schmidt, soorten die in Nederland niet voorkomen. Blijkbaar is er overeenkomst wat betreft de concurrentie, die *Montia* van andere soorten ondervindt en is deze concurrentie van overwegende betekenis, want vele groeiplaatsomstandigheden (klimaat, koud water) zijn stellig in de Alpen anders dan op de vindplaatsen in Nederland.

Zowel in Noord Drente als in Noord Twente komt deze subspecies ook op veel minder exclusieve standplaatsen voor. Clason (1953) gaf een voorbeeld van Noord Drente, waarbij in de kussens van Montia ook de landvorm van *Batrachium aquatile* Dum., *Peplis portula* L., *Callitriche hamulata* L., *Bidens cernuus* L., *B. tripartitus* L., *Epilobium parviflorum* Schreb., *Myosotis scorpioides* L., *Stellaria graminea* L., *Juncus bufonius* L., *Eleocharis palustris* R. et Sch., *Glyceria fluitans* R. Br., *Alisma plantago-aquatica* L. en *Sparganium erectum* L. optraden. Dit is daar de gewone pionierbegroeiing van greppels in het cultuurgebied, waarbij de *Montia* zich slechts beperkte tijd kan handhaven. Het is wel zeer waarschijnlijk, dat *Montia* hier een biotoop gevonden heeft, waar zij zich ook in het cultuurgebied heeft kunnen vestigen. De opgaven van Diemont c.s. (1940) van *Montia minor* in Drente hebben stellig grotendeels betrekking op de subspecies *rivularis*. In Noord Twente groeien de planten op soortgelijke standplaatsen, b.v. noteerde ik in greppels in het weiland van het brongebied van de Mosbeek, naast de *Montia*, *Callitriche* sp., *Lysimachia nummularia* L., *Glyceria fluitans* (L.) R. Br., *Cardamine amara* L., *Lotus uliginosus* Schkuhr en *Lemna minor* L.

Herbariummateriaal van nederland

Drents District: Noord-Drente: Midlaren, veenachtige grond, 24–5–1906, J. Th. Henrard, [L]. Langelo, 12–4–1914, A. v. Veldhuizen, [GRO]. Ballo, Lamaden, slootje in lemig zand, kussenvormige groeiwijze, 14–9–1953, E.W. Clason, [GRO]. Vries-Zuidlaren, greppel langs de hoofdweg bij de Drentse A, 22–5–1953, E. W. Clason, [GRO] (Fig. 6 nr 5). *Drente*: Weerdinge, 7–1890, Exc. *Noord-Twente*: Ootmarsum, rand slootje langs de weg, stengels dreven gedeeltelijk, 6–1905, D. Lako & M. J. Blijdenstein; 10–6–1905, P. J. van Breemen, [L]; 22–6–1905, Ed. & Tk.; Sprengendal, Meerbekke, 4–6–1933, F. P. Jonker & S. J. van Ooststroom nr 5548 (*M. lamprosperma* Cham. en *M. fontana* L. ssp. *lamprosperma* Lindb.), [L]; 8–1946, J. Kern (*M. lamprosperma* Cham.), [L]; Sprengendal, aan de beek, 17–6–1942, Utr. biologen, [U]; in vers gegraven greppel, kussenvormige groeiwijze, landvorm, 14–9–1952, E. W. Clason, [GRO]; Hezinge, achter watermolen „Frans", dicht bij Duitse grens, sloot in weiland, 31–10–1954, en weiland in brongebied Mosbeek, 31–10-1954, E. W. Clason, [AMD, GRO, L], Denekamp, 6–1900, H. W. Peteri nr 670, [AMD]; 12–6–1917, M. Kruseman, [AMD].

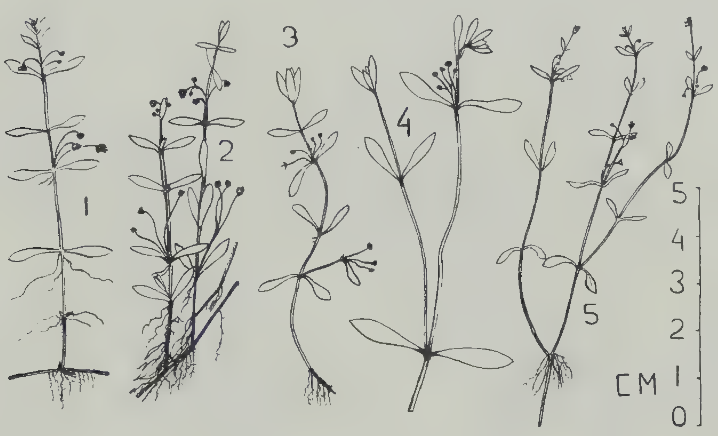

Fig. 6. *Montia fontana* L. ssp. *rivularis* (Gmel.) S. et M. 1. Putten/Ermelo, beekjes op de heide, Van der Trappen. 2. Wolfheze, sprengen, 15–6–1915, Van Embden [L]. 3. Uchelen, sprengen, 5–1878, V. d. S. Lacoste [L]. 4. Wenum, in een sloot, Kok Ankersmit [L]. 5. Vries-Zuidlaren, greppel, 22–5–1953, E. W. Clason [GRO].

Gelders District: Epe, Wisselse Ven, op boomstammen in een sloot, 28–6–1920, H. Uittien, [U]. Harderwijk, sloten iets lopend water, 18-5-1899, H. J. Kok Ankersmit; 6–1866, R. Bondam. Putten/Ermelo, beekjes op de heide, ongedateerd, Van der Trappen (Fig. 6 nr 1). Putten, Schoonderbeek, sloot, ongedateerd, A.A. Dornseiffen. Hoenderlo, sprengen, 18–10-1900, J. W. C. Goethart & J. Ensink A. Jzn., [AMD], Apeldoorn, 6–1953, H. J. Kok Ankersmit; buurt Wormingen, sloot, 28–5–1875; id. sloot te Wenum, kolossale planten, rechtop, dicht aaneengesloten, minstens 1/2 voet boven water uitstekend, 19–6-1899 [NBV, L] (Fig. 6 nr 4); beekjes achter Het Loo, 6–1834, J. Wttewaal; sprengen, J. Koorneef; 7–1858, Oudemans. Leuvenumse Bos, bij de Zwarte Boer, sloot in het veentje, 11–6–1905, D. F. van Slooten, [U]. Soeren, bois, E. Piaget; 8–1909, Poldervaart; 7–1897, H. Heukels. Loenen, drijvend in stromende beekjes, 14–6–1880, H. J. Kok Ankersmit, [L]; 1880, H. W. Groll. Uchelen, oorsprong beek De Grift, 8–1854, J. S. v. d. Sande Lacoste; sprengen, 5–1878, D. Lako, [L] (Fig. 6 nr 3). Arnhem, Sijpenberg, C. Bergsma, [AMD, U]; Van Hall. Velp, C. A. Bergsma; tussen Beekhuizen en Klarenbeek, 6-1828; op Beekhuizen, 9–1866. v. d. Sande Lacoste (*M. fontana β major* Schrad.). Wolfheze, beek, 8–1847, Boursse-Wils; in beek, 1847, v.d. Sande Lacoste; in sloten van het bos, 7–1856, Oudemans; bos, 7-1857, F. A. Hartsen; bos, 7–1879, F. W. van Eeden; sprengen van de Heelsumer beek, 15–6–1915, W. C. van Embden, [L] (Fig. 6 nr 2). Heelsum, half droge sloot, 7–1830, Buse. Wageningen, Keyenberg, in snel stromend water, 30–7–1833, Wttewaal; in een sloot, L. Bakhuizen, [U]; 5–1883, W. G., [L]. Ede, veensloot, 7–1900, J. Valckenier Suringar, [L], Van Vloten, [L]; Doesburg (bij Ede), 5–5–1902, Goethart, Janse & Jongmans, [L]. Renkum, in rivulis, 6–1851, Buse; beek, 6–1883, W. G. [L]; 17–6–1897, Biol. Stud. Leiden en F. J. Struykenkamp, [L]. Hilversum, de vaart, in stromend water, 6–7–1872, v. d. Sande Lacoste nr 936, [AMD, GRO, L]; beek, 3–6–1899, Th. Weevers.

Subcentreuroop District: De Lutte, in een beekje, 28–8–1895, Exc. Enschede, Aanveense weg, 21–5–1898, Goethart & Vuyck. Lonneker, 1–5–1904, M. J. Blijdenstein. Glanerbrug/Losser, in een sloot bij de Elsbeek, 21–5–1898, Goethart & Vuyck (*M. minor*). Glanerbrug, Rotermansvonder, 21–5–1898, Goethart & Vuyck

(*M. minor* f. *rivularioides*). Winterswijk, 29–5–1904, Rust. Haaksbergen, drooggelopen heisloot, 7–1891, D. Lako; idem, D. Lako & Chr. C., [L]; venen, 8–1905, W. W. Schipper, [L]. Doetinchem, 22–5–1899, G. van Vloten (*M. minor*), [L]. Nijmegen, A. de Beyer (*M. fontana β minor*), [NBV, GRO]. Afferden, 20–6–1928, Joh. Jansen. Malden, 20–6–1931, Joh. Jansen.
Kempens District: Eindhoven, 6–?, Forsten (*M. rivularis* var. *fontana*).

Voorkomen buiten nederland

Aan de hand van literatuur en materiaal in de Nederlandse herbaria vormde ik mij het volgende, voorlopige beeld van de verspreiding. N. Amerika. Bohemen, zie Fig. 7 nr 2. Zwitserland. Duitsland, zie Fig. 7 nr 1. Saarland. België. Frankrijk. Portugal. Zuid- en Midden-Engeland. Ierland. Australië ?Noord-Afrika.

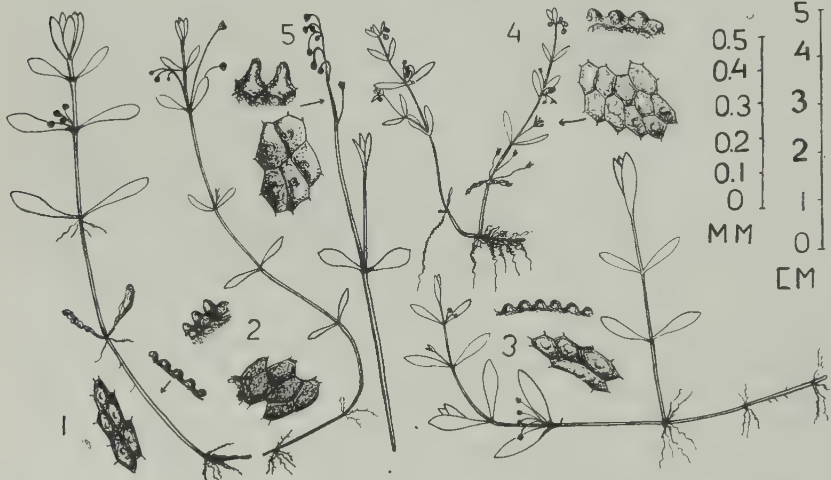

Fig. 7. *Montia fontana* L ssp. *rivularis* (Gmel.) S. et M. van buiten Nederland. 1. Westfalen, in Wiesengraben, 26–6–1883, Demandt, [AMD]. 2. Bohemen, Carlsbad, 24–8–1860, F. A. Hartsen, [L]. 3. Portugal, Monchique, 22–6–1936, A. Kostermans & W. Kruyt, [L]. 4. Portugal, Manteigas, 30–4–1936, A. Kostermans & W. Kruyt, [L]. 5. N. Amerika, Washington, 28–5–1893, W. N. Suksdorf, [L].

Enkele opmerkingen over de taxonomie van montia fontana L. buiten nederland

Van over de gehele wereld verspreide punten zijn planten bekend geworden, die men tot *M. fontana* L. in de door mij gebruikte begrenzing kan rekenen. Pax und Hoffman (1932) vermelden, dat *M.*

Fig. 8. Vindplaatsen in Nederland, waarvan het herbariummateriaal vermeld is: ↓ *M. fontana* L. ssp. *fontana* var. *fontana*. ● *M. fontana* L. ssp. *fontana* var. *chondrosperma* Fenzl. + *M. fontana* L. ssp. *rivularis* (Gmel.) S. et M. Floradistricten volgens Van Soest (1929): DUIN = duin–, WAD. DUIN = waddenduin–, OH = oostelijk haf–, WH = westelijk haf–, DR = Drents, GE = Gelders, S = subcentreuroop, FL = fluviatiel, KE = Kempens, L = löss–, en KR = krijtdistrict.

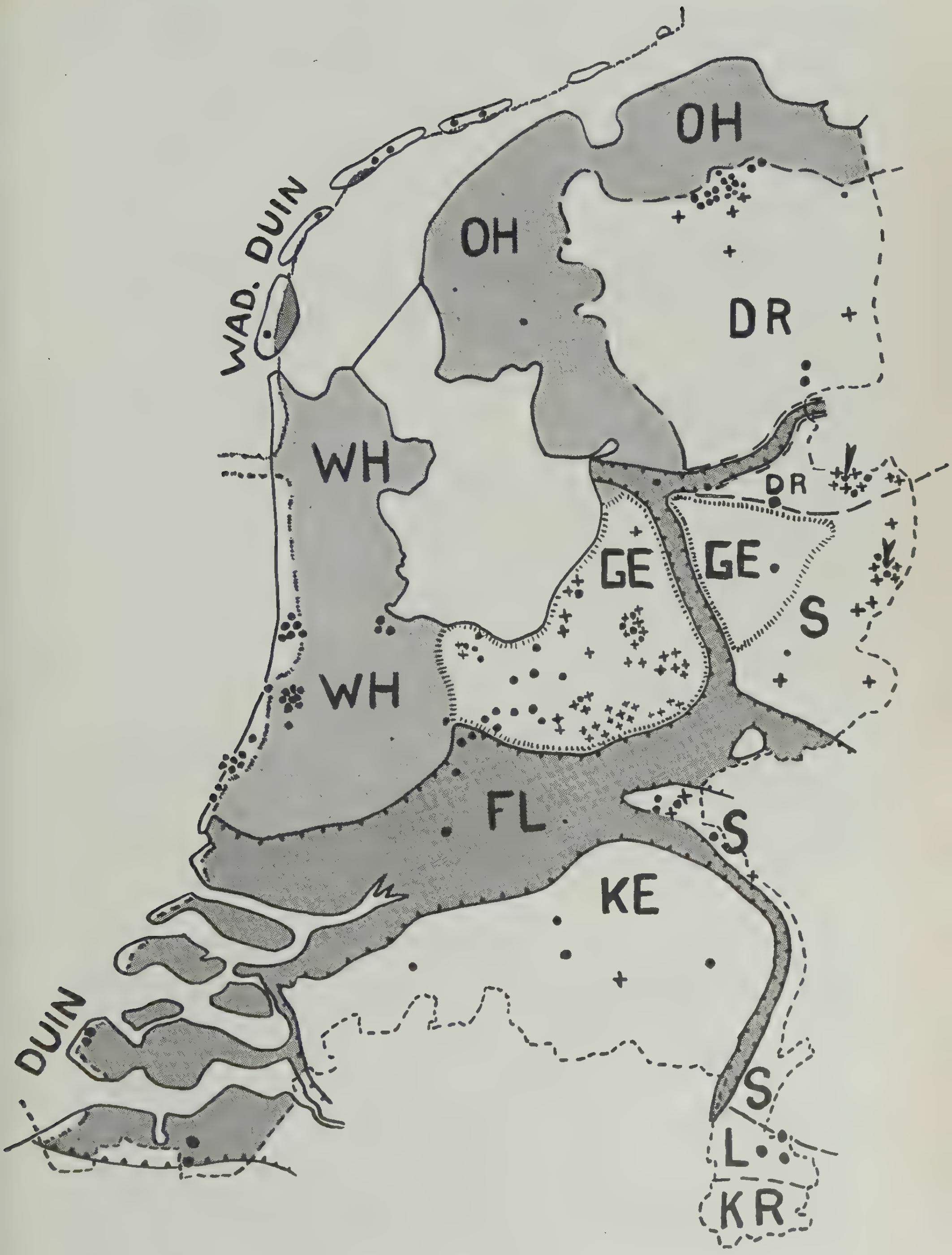

Fig. 8

fontana L. dikwijls in drie kleinere soorten gesplitst wordt, nl. *M. minor* Gmel., *M. lamprosperma* Cham. en *M. rivularis* Gmel., terwijl zij *M. limosa* Decker als nieuw beschreven vermelden. Deze soorten zijn in het voorgaande reeds besproken. Von Poellnitz (1941) heeft vijf kleine soorten, nl. de zo even genoemde, waarbij *M. limosa* Decker als de landvorm van *M. rivularis* Gmel. beschouwd wordt, en bovendien een Amerikaanse soort *M. dipetala* Suksd. met slechts twee kroonslippen.

In Noord-Amerika onderscheiden Fernald and Wiegand (1910) „three clearly defined species", die ook volgens hun plaat 84 (gereproduceerd in Fig. 9) overeenkomen met onze taxa. Rydberg (1932) heeft voor hetzelfde gebied bovendien nog zes endemische soorten langs de noordwestkust. Volgens R. zijn de *M. minor*-planten van Amerika forser dan die van Europa, hetgeen ik bij een herbariumspecimen van Washington, L. 914.74.268 ook kon constateren. Het zaad van *M. rivularis* heeft volgens R. geen of slechts „flat and low tubercles", zie Fig. 7 nr 5.

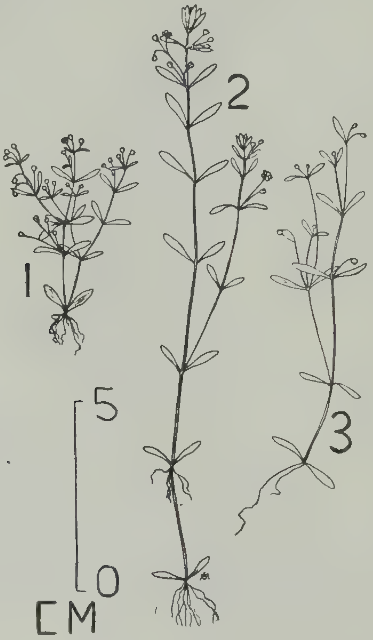

Fig. 9. De afbeelding van Fernand and Wiegand (1910). 1. *Montia minor* Gmel. 2. *Montia rivularis* Gmel. 3. *Montia lamprosperma* Cham.

Wat de Britse eilanden betreft, onderscheiden Clapham c.s. (1952) met medewerking van S. M. Walters drie soorten, nl. *M. verna* Necker, *M. lamprosperma* Cham, en *M. lusitanica* Sampaio. Echter heeft Walters (1953) in plaats van *M. lusitanica* Sampaio de ssp. *intermedia* (Beeby) W. gesteld. Hij meent, m.i. ten onrechte, dat de naam *M. rivularis* Gmel. niet meer bruikbaar is (zie boven blz. 248). Van de knobbels op de rug van het zaad bij laatstgenoemde soort schrijft W.: „cells on each side of keel bearing small but relatively narrow and high tubercles, one in centre of each cell", hetgeen overeenkomt met de kratervormige puisten, die voorkomen bij onze ssp. *rivularis*. W. onderscheidt voorts nog een ssp. *variabilis* W. die van zijn ssp. *intermedia* onderscheiden zou zijn door slechts kleine en lage knobbeltjes op de rug; dergelijk zaad komt ook bij de Nederlandse planten voor, maar ik heb niet gevonden dat naar dit criterium twee gescheiden taxa aanwezig zijn.

In continentaal Europa heeft men zich na de studie van ASCHERSON (1872) hoofdzakelijk gehouden aan *M. minor* GMEL., *M. lamprosperma* CHAM. en *M. rivularis* GMEL.; zie voor synoniemen ASCHERSON und GRAEBNER (1915). De landvorm van *M. rivularis* GMEL. is niet onopgemerkt gebleven, getuige *M. limosa* DECKER (1927) en *M. rivularis var. lamprosperma* BECK (1890) non CHAM.

HYLANDER (1945) heeft voor Scandinavië *M. verna* NECKER en *M. rivularis* GMEL., met welke laatste hij en andere Scandinaafse auteurs kennelijk de var. *fontana* bedoelen. Het schijnt onzeker te zijn of *M. rivularis* GMEL. op het vasteland van Scandinavië voorkomt. De planten aldaar hebben blijkbaar glad, glinsterend zaad, waarbij er ook zijn, die de indruk wekken overblijvend te zijn (b.v. L. 948, 146. 421) en dergelijke planten zijn ook elders in Europa gevonden, zoals in Tirol (L. 910. 111. 1253 en 1256) en de Pyreneeën (AMD. 009246). ASCHERSON (1872) heeft zich reeds afgevraagd, of er geen overblijvende planten waren met gladde, glinsterende zaden, maar kon die in het Berlijnse herbarium niet vinden.

SAMPAIO (1912) heeft de planten van Portugal tot een eigen soort *M. lusitanica* gebracht, die zich voornamelijk van de soorten van GMELIN (1805) zou onderscheiden door sterk ontwikkelde knobbeltjes op de rug van het zaad. Van vier planten uit Portugal, die ik kon onderzoeken, was er één geheel identiek met onze ssp. *rivularis*, zie Fig. 7 nr 3, terwijl de andere drie wel sterk ontwikkelde uitsteeksels hadden aan de rugkant van het zaad, maar niet zodanig, dat ze niet eveneens tot ssp. *rivularis* gerekend zouden kunnen worden, doch de habitus van de laatste drie is wel iets afwijkend, zie Fig. 7 nr 4.

4. AANTEKENINGEN OVER DE PLASTIEK

BRAUN (1858) gebruikte het woord „Plastik" bij de bloemen voor de mogelijkheden om te verschillen in vorm bij eenzelfde grondplan wat betreft het aantal en de rangschikking der bloemdelen. SCHOUTE (1938) meende, dat de term „plastics" van nut zou kunnen zijn in de algemene morphologie „to denote the range of variation of differentiation". Bij alle *Montia*-planten is er één grondplan, o.a. met decussate bladstand, maar de plastiek is zeer verschillend. Reeds LINNAEUS (1737) merkte op, dat de planten van zijn soort op „wonderbaarlijke" wijze „ speelden" wat de grootte betreft.

A. BESCHRIJVING VAN DE PLASTIEK

Plastiek van de wortel

De hoofdwortel is bij vruchtrijpe planten van de ssp. *fontana* niet opvallend, bij de ssp. *rivularis* reeds vroegtijdig afgestorven en, evenals het onderste deel van de stengel, afgerot. De vele bijwortels komen eerst bij de knopen en daarna ook verder naar beneden langs de internodia te voorschijn. Bij de eenjarige planten van de ssp. *fontana* vindt men alleen wortels die in de grond dringen. Bij de overblijvende planten van de ssp. *rivularis* zijn er ook, of alleen, bijwortels, die in de lucht stijf uitstaan dan wel in het water zweven; ook aan stengelleden met groene bladen zijn deze wortels dikwijls te vinden.

Plastiek van de stengel

De stengel is kruidachtig en bij welig ontwikkelde planten kan men de centrale cylinder in het doorschijnende schorsweefsel zien liggen (geslachtskenmerk bij Ascherson und Graebner 1915). Bij de planten van de var. *chondrosperma* met beperkte levensduur blijven de stengels meestal zo kort, dat zij min of meer rechtop staan. Bij de overblijvende planten van de ssp. *rivularis* is de bouw van de stengel weinig anders, zie Graebner (1895), maar hier worden de stengels vrijwel steeds zo lang, dat zij doorzakken, waarbij ze opstijgend worden met afrottende ondereinden, voorzover ze niet in het water zweven. Zie ook Fig. 2.

Zijtakken worden veelvuldig gevormd bij planten onder niet te ongunstige groeiomstandigheden. Deze zijtakken ontwikkelen zich afwisselend in een van de beide oksels van de bladparen, dikwijls gescheiden door een bladpaar zonder zijtak. Ze groeien dikwijls even sterk als de hoofdassen, waardoor bij de rechtopstaande planten van de ssp. *fontana* de vertakking dikwijls min of meer vorksgewijs is, terwijl bij de planten van de ssp. *rivularis* de zijassen dikwijls zelfstandig worden door afsterven van de ondereinden.

Linnaeus (1737) hecht grote taxonomische waarde aan de bloeiwijze. Velenowsky (1910) beschouwt de bloeiwijze als een bijzondere modificatie van een schicht, die hier feitelijk de voortzetting is van het voorafgaande stengellid. De bloeiwijzen staan evenals de zijtakken afwisselend in slechts één van de beide oksels der opvolgende bladparen, terwijl vooral bij geëtioleerde groei dikwijls een bladpaar zonder bloeiwijze voorkomt. De bloeiwijzen beginnen met twee gesteelde bloemen, die uit de oksels te voorschijn komen. De volgende bloemen staan afzonderlijk afwisselend aan weerszijden van de bloeias. In de oksel zit min of meer ter zijde een klein schutblad, dat Velenowsky beschouwt als één der beide voorbladeren, die meestal bij Dicotylen voorkomen; dit schutblad is bij de Nederlandse planten dikwijls afwezig. Uit de bladoksels tegenover die met een bloeiwijze wordt dikwijls een zijas gevormd, die de oorspronkelijke stengel sympodiaal verlengt. Bij de overblijvende planten van de ssp. *rivularis* gaat de sympodiale verlenging van de stengel steeds door, zodat men aan de top van planten op niet te ongunstige groeiplaatsen steeds goed ontwikkelde groene bladparen vindt, waarbij de bladen van elk bladpaar even groot zijn. Bij de kortlevende planten van de ssp. *fontana* komt de sympodiale groeiwijze tot stilstand en bij voldoend gunstige groeiomstandigheden groeien dan de laatstgevormde bloeiwijzen opvallend eindelings uit. Niet alleen dat de vorming van een overtoppende zijas achterwege blijft, maar dikwijls ontwikkelt het blad, in welks oksel de zijas had moeten staan, zich slechts tot een klein vliezig schutblad; dit kenmerk werd reeds gebruikt door GRENIER et GODRON (1848). Wanneer de planten op een iets beschaduwde plaats staan dan wel door onderlinge concurrentie of door soortvreemde buurplanten beschaduwd raken, kan een geëtioleerde groei optreden, waarbij de stengelleden lang worden en de bladen klein blijven; met deze plasticerende factor dient men bij de beoordeling der planten rekening te houden.

Plastiek van het blad

De bladen aan de top van de stengel en vlak onder de eindelingse bloeiwijze zijn reeds bij de stengel ter sprake gekomen. Bij ssp. *fontana* worden de planten en vooral de bladen reeds voor het beëindigen van de groei in de voorzomer rossig-geel. Bij de ssp. *rivularis* blijven de topbladen van de overtoppende zijassen steeds groen en goed ontwikkeld (Fig. 12 nr 1). Op deze verschillen wordt reeds gewezen door GMELIN (1805) en na hem o.m. door ASCHERSON (1872) en door RYDBERG (1932). Verder heb ik geen constant voorkomende verschillen tussen de bladen van beide ssp. kunnen vinden, hoewel VAN HALL (1825) en VAN EEDEN (1872 en 1881) die voor de Nederlandse taxa opgeven. De iets vlezige bladschijven zijn eerst lancetvormig-langwerpig en wanneer zij goed uitgroeien is er beneden een versmald gedeelte, dat opgevat kan worden als verbrede bladsteel of aanleiding is om te spreken van spatelvormig (Fig. 12 nr 4). De bladvoet is halfstengelomvattend en beide bladvoeten van een bladpaar zijn ter weerszijden van de stengel iets vergroeid (Fig. 12 nr 1); dat de mate van vergroeid zijn een onderscheid zou uitmaken tussen de taxa, cf. GMELIN (1805) en vele auteurs na hem, is mij bij de Nederlandse taxa niet gebleken.

Plastiek van de zaadhuid

RYDBERG (1932) maakt in Noord Amerika bij het onderscheiden van zijn negen Montia-soorten, die alle onder *M. fontana* L. vallen, zoals de soort door mij begrensd wordt (zie stuk 3), ook gebruik van bloem- en vruchtkenmerken. Voorzover ik kon nagaan, is dit bij de Nederlandse taxa niet mogelijk. Van des te meer belang is ook bij ons het zaad, zoals door OUDEMANS (1861) reeds werd vastgesteld. VON CHAMISSO (1831) was de eerste, die meende Montia-taxa uitsluitend te kunnen typeren met zaadkenmerken.

De grootste doorsnede van het zaad (Fig. 10) is bij benadering rond; in het vlak van deze doosnede bevindt zich de geelbruine tot witachtige navel en daartegenover de rugkant. De rugkant versmalt zich ter ener zijde naar de navel tot een meer of minder duidelijke kam; ter andere zijde van de navel bevindt zich de zone, waar bij de campylotrope zaadknop de mikropyle was, op deze plek kan het zaad iets ingesnoerd zijn en dan is de omtrek een weinig niervormig. De zijkanten ter weerszijden van de grootste doorsnede zijn steeds meer of minder afgeplat, zodat de snijvlakken loodrecht op de grootste doorsnede de ellipsvorm benaderen. De vorm van het zaad is ongetwijfeld mede afhankelijk van de mate waarin perisperm en embryo zich onder invloed van de uitwendige omstandigheden hebben kunnen ontwikkelen.

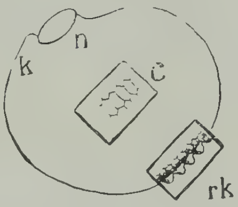

Fig. 10. Zaadvorm bij *Montia fontana* L. n = navel; k = kam; rk = rugkant; c = centrum van de afgeplatte zijkant.

De doffe zaden van de var. *chondrosperma* lijken dikwijls groter dan de glanzende zaden bij de andere beide taxa. Bij nameten blijken de verschillen bij de Nederlandse planten gering; dit blijkt ook uit de afbeeldingen van Beijerinck (1947). Ook de vorm der zaden en de kleur van de navels zijn taxonomisch niet bruikbaar. De kleur der zaden lijkt mij, in tegenstelling met Kloos (1947), eveneens niet van belang. Bij goed uitgerijpte zaden is de kleur steeds zwart; slechts bij de dunne zaadhuid van de ssp. *fontana* var. *fontana* kan de bruine inhoud der cellen iets doorschemeren, maar ik betwijfel of deze zaden dan goed rijp zijn. Het is volgens mij de hoedanigheid van de zaadhuidcellen, die taxonomisch van waarde is.

De anatomie van de zaadhuid is onderzocht door Lohde (1874/5) en Ohlendorf (1907), doch vooral door Meunier (1890). Van belang is voor ons doel alleen de epidermis van het buitenste integument, waarvan de cellen zich sterk vergroten, zodat tenslotte de voegen reeds bij loupe-vergroting als onregelmatige veelhoeken op de buitenkant van het zaad zichtbaar zijn. Bij de geknobbelde zaden staan deze cellen naar buiten bol uit, soms hebben zij een kratervormige puist. Van

Fig. 11. Knobbels van het zaad van *Montia fontana* L. in Nederland. Rugkant in profiel en centrum zijkant van boven gezien. Ssp. *fontana* var. *chondrosperma* Fenzl.: 1. Groningen, 1846, Stratingh. 2. Groningen, Cayaux. 3. Haren, 1933, Buwalda. 4. Ameland, 1869, Holkema. 5. Peize, De Gavere. 6. Eelderwolde, 1869, Van Hall. 7. Groningen, h. Dassen. 8. Dalfsen, 1905, Lako. 9. Utrecht, 1906, Van Embden. 10. Haarlemmerhout, 1868, Van Eeden. 11. Leyderdorp, ?Molkenboer. 12. Leiden, 1946, De Jongh c.s. 13. Domburg, 1877, Lako. 14. Sas van Gent, 1855, Walraven. 15. Apeldoorn, Kok Ankersmit. 16. Dalen, Kern. Ssp. *rivularis* (Gmel.) S. et M.: 17. Vries-Zuidlaren, 1953, Clason. 18. Ballo, 1952, Clason. 19. Ootmarsum, 1905, Van Breemen. 20. Beekhuizen, 1828, Van Eeden. 21. Arnhem, Sijpenberg, Van Hall. 22. Hoenderlo, 1890, Goethart en Vuyck. 23. Hilversum, 1872, V. d. S. Lacoste. 24. Varsseveld, 1902, Des Tombes. Ssp. *fontana* var. *fontana*.: 25. Ootmarsum, 1934, Heimans. 26. Vasse, 1946, Joh. Jansen. 27. Lonneker, 1905, Blijdenstein. 28. Vasse, Mosbeek, 1954, Clason.

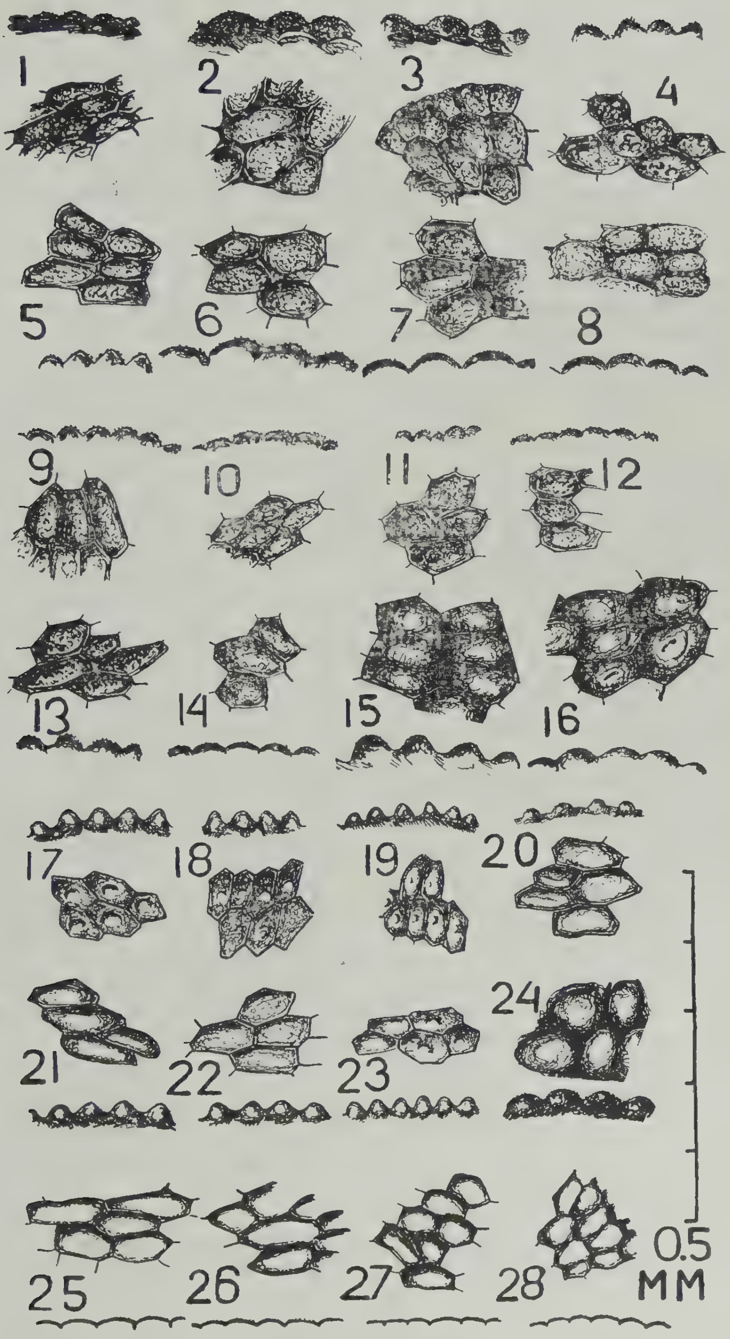
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Fig. 11

binnen zijn de wanden van de knobbels verdikt met loodrecht op het buitenoppervlak staande structuren, die MEUNIER (1890) stalactieten noemt. De boveneinden van de stalactieten zijn van buiten waarneembaar als een net van gekronkelde draden; bij de dunne zaadhuid van de var. *fontana* zijn de draden vanzelfsprekend minder duidelijk. De knobbels zijn steeds het sterkst ontwikkeld aan de rugkant en het minst in het centrum van de afgeplatte zijkanten van het zaad. Om het zaad te karakteriseren is het daarom voldoende enkele cellen van die plaatsen in beschouwing te nemen. In de afbeeldingen van Fig. 3, 7 en 11 zijn de centrumcellen daarom van boven gezien en de rugcellen in contourlijn getekend (rechthoeken in Fig. 9.) zoals men die onder het microscoop waarneemt, daar de zaden van nature op een der afgeplatte zijkanten liggen.

Ssp. *fontana* var. *chondrosperma* (Fig. 11 nrs 1 - 16). Grootste doorsnede van het zaad 0.9 – 1.1 mm. MEUNIER (1890) behandelt kennelijk het zaad van deze varieteit. De dofheid wordt veroorzaakt door kleine uitgroeisels van de cuticula, die bij de zaden van de andere taxa althans in het centrum steeds ontbreken. Deze uitgroeisels zijn bij 150 × vergroting duidelijk zichtbaar. Van groot belang is, dat de dofheid met het blote oog of geringe vergroting gezien duidelijk is, doch bij sterkere vergroting verdwijnt, daar dan de cuticula tussen de uitgroeisels glimlichten vertoont. Deze glimlichten hangen uiteraard sterk af van de gebruikte belichting. Uit de afgebeelde profielen van de rugcellen blijkt, dat bij de Nederlandse zaden de vorm en de grootte van de knobbels uiteenloopt. Bij de cellen in het centrum komt ook voor, dat op de knobbels kleine indeukingen aanwezig zijn, Fig. 11 nrs 4, 6, 11. Slechts bij nr 5 kan men van scherpe knobbels spreken, zoals VAN EEDEN (1872) dat gedaan heeft. De nrs 1, 2, 3, 5, 6, 7 van Fig. 11 zijn van planten uit de buurt van Groningen en laten zien dat ook in één streek planten naast elkäar voorkomen met meer en minder geprononceerde knobbels.

Ssp. *rivularis* (Fig. 11 nrs 17 – 24). Grootste doorsnede van het zaad 0.8 – 1.0 mm. Reeds met het blote oog gezien is er op de zijkanten glans en de cellen aldaar hebben geen uitgroeisels op de cuticula, terwijl de draderige structuur van de diepere lagen van de celwand goed zichtbaar is. Deze centrumcellen kunnen bol staan, dus duidelijke knobbels vormen, of alleen maar een kleine puist hebben of vrijwel vlak zijn. De puisten worden naar de rugkant geleidelijk groter en lopen dikwijls puntiger toe dan die bij var. *chondrosperma*, men kan dan van „scherp" spreken. Deze scherpe rugpuisten hebben dikwijls wel uitgroeisels op de cuticula, zijn derhalve met het blote oog gezien dof.

Ssp. *fontana* var. *fontana* (Fig. 11 nrs 25 – 28). Grootste doorsnede van het zaad 0.9 – 1.1 mm. Reeds met het blote oog gezien is het zaad sterk glanzend (glinsterend). De centrumcellen staan weinig bol uit of zijn nagenoeg geheel vlak; uitgroeisels van de cuticula zijn afwezig, draderige structuren in de wand zijn afwezig of althans niet goed ontwikkeld. Op de gladde zijkanten vormen de voegen der veelhoekige cellen een nettekening, zoals reeds beschreven door VON

Chamisso (1831). De rugcellen staan slechts weinig bol en hierop zijn ook wel eens uitgroeisels zichtbaar. Hylander (1945) schrijft, dat de zaden van de noordelijkste planten meer relief vertonen dan die uit Zweden met „reif beinahe ganz strukturlosen, ausserordentlich glänzenden Samenschalen, die ausserdem so spröde sind, dass sie bei den meisten Herbarexemplaren vor der Reife zerbrochen sind". Dit laatste is ook meermalen bij de Nederlandse zaden het geval. Hultén (1944) meldt wat dit betreft bij de zaden van Aljaska, de type-vindplaats van *M. lamprosperma* Cham., „a wide variation".

Binnen de drie door mij onderscheiden taxa is de zaadhuid even plastisch als de stengel. Men kan dit beschouwen als een gevolg van het verschillend sterk uitgroeien van de zaadhuidcellen, nl. het sterkst bij var. *chondrosperma*, minder sterk bij ssp. *rivularis* en het minst sterk bij var. *fontana.*

B. Oorzaken van de plastiek

De oorzaken van de plastiek kunnen eenerzijds gedacht worden als direct en voor iedere individuele plant opnieuw uitgaande van de standplaats, vooral wat licht- en waterverhoudingen betreft. Anderzijds hebben de planten een overgeërfde aanleg, waardoor de plastiek bepaald en begrensd wordt. Walters (1953) merkt op, dat beide groepen van oorzaken bij *Montia* taxogenetisch gelijkgericht kunnen werken. Bij een erfelijk beperkte levensduur zal men kleine planten verwachten, maar tevens dat deze planten hun ontwikkelingskansen vooral vinden op slechts tijdelijk vochtige grond, waar planten met een minder beperkte levensduur niet tot volle ontplooiïng van hun vorm kunnen komen. Deze redenering gaat op voor de eenjarige ssp. *fontana*; voor de overblijvende ssp. *rivularis* is een soortgelijke redenering mogelijk. De vraag rijst van welke aard de taxa onder de soort *M. fontana* L. zijn, hoe de kenmerkende plastiek ontstaat en hoe de taxa als zodanig bestaan blijven.

Standplaatsinvloeden; transplantatieproeven

De varieteit *chondrosperma* (*M. minor* Gmel.) en de subspecies *rivularis* (*M. rivularis* Gmel.) zijn elk aan een eigen biotoop gebonden. Daardoor heeft men zich van oudsher afgevraagd of deze taxa wel erfelijk bepaald zijn, cf. Van den Bosch (1850) en Vuyck (1901).

Blijdenstein (1906) nam een proef met typische planten (Fig. 12 nr 3) van de var. *chondrosperma,* die hij in April vond in een tuin op vochtige zandgrond te Enschedé (Twente), zie bij herbariummateriaal blz. 254. Blijkens aantekeningen op het herbariumvel zette hij de planten 20 à 30 cm diep onder water en in Mei hadden de plantjes lange, draderige stengels gevormd (Fig. 12 nr 2). Daardoor deden ze aan de ssp. *rivularis* denken, maar onder andere door het niet optreden van adventief-wortels is er toch geen sprake van verwarring met deze subspecies.

Kerbert en Molkenboer, zie Vuyck (1901) tekenden op het vel van een herbariumexemplaar, verzameld in de weilanden bij Oegstgeest, ongedateerd (vermoedelijk 1836), in Herbarium Van Hall, aan: ,,Het schijnt alsof aldaar de *M. minor* langzamerhand in *M. rivularis* overgaat". Een van hun exemplaren is afgebeeld in Fig. 12 nr 1 en maakt de indruk van gegroeid te zijn op natte veengrond maar vertoont de typische eindelingse bloeiwijze van var. *chondrosperma*, zodat er geen sprake is van overgang naar ssp. *rivularis*. Blijkbaar heeft deze kwestie de aandacht gehad van de tijdgenoten, want van dezelfde omgeving is materiaal verzameld door V. d. S. Lacoste 4–1836, Molkenboer 5–1836, J. Schuurmans Stekhoven, Boursse Wils en Oudemans, waarbij ik geen planten kon vinden van de ssp. *rivularis*, terwijl de typische forse planten van nat veen met dof, geknobbeld zaad van de varieteit *chondrosperma* aanwezig zijn. Het gelukte mij niet om van planten van de varieteit *chondrosperma* onder vochtige omstandigheden iets te kweken, dat op ssp. *rivularis* geleek; de planten vergeelden bovendien steeds vroegtijdig en stierven af.

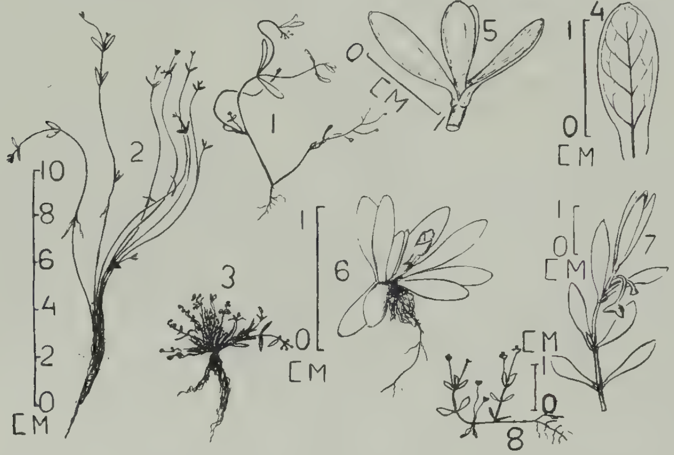

Fig. 12. Plastiek van *Montia fontana* L. 1–3. *M. fontana* L. ssp. *fontana* var. *chondrosperma* Fenzl. 1. plant van natte veengrond bij Leiden, Molkenboer en Kerbert. 2. plant na inundatie, Blijdenstein (1906). 3. plant vóór inundatie, Blijdenstein (1906). 4. Blad van *M. fontana* L. 5–8 *M. fontana* L. ssp. *rivularis* (Gmel). S. et M. 5. bebladerde stengeltop (landvorm in de winter). 6, 7 en 8, zie tekst, deze en volgende blz.

Bij de planten van de ssp. *rivularis* heb ik de invloed van droge standplaats nagegaan. Ik gebruikte daarvoor planten van Noord Drente (Ballo) en Noord Twente (Ootmarsum), zie GRO., die zich volkomen eender gedroegen. Op 15–4–1953 waren de bebladerde toppen van deze planten (Fig. 12 nr 6) nauwelijks 1 cm, maar toch groen; de eerste bloemknoppen waren toen gevormd. Ook bij deze kleine plantjes hadden zich de kenmerkende overtoppende zijassen ontwikkeld. Op 15–5–1953 waren de planten na regenachtig weer uitgegroeid tot ongeveer 3 cm en boven de uitgebloeide bloemen waren de overtoppende zijassen sterk ontwikkeld (Fig. 12 nr 7). Op 6–6–1953, na dróog weer, waren de inmiddels gegroeide stengeldelen slecht ontwikkeld en grotendeels vergeeld, maar — in tegenstelling met planten van de var. *chondrosperma* in gelijke omstandigheden — waren de allerbovenste blaadjes aan de overtoppende zijassen toch nog groen gebleven, terwijl in dit extreme geval twee tot drie bloemen boven de laatste bladeren uitstaken (Fig. 12 nr 8). Verwarring van deze zeer kleine plantjes met die van de var. *chrondosperma* is uitgesloten.

Op 6–6–1954 verzamelde ik planten van de var. *fontana* (Fig. 2 nr 1) in een elzenbosje op brongrond langs de Mosbeek bij Vasse, zie herbariummateriaal blz. 251. Deze planten kweekte ik in een stenen waskom en kon ze daarin bevrijd van concurrentie tot het eind van de zomer in het leven houden, terwijl ze op de natuurlijke standplaats reeds veel eerder verdwenen waren. De groeikracht was echter gering en niet te vergelijken met die van de ssp. *rivularis*, die in de tweede helft van de zomer welig groeien, zich sterk vertakken en eventueel kussenvormig tegen elkaar op buiten het water omhoog komen. Bij het verzamelen hadden de planten van de var. *fontana* eindelingse bloeiwijzen, waaronder hier en daar een ongelijk bladpaar. Onder de gunstige omstandigheden in de waskom vormden vele planten een overtoppende zijas (Fig. 2 nr 2), hetgeen zich gedurende de zomer enkele keren herhaalde, waarbij zich ook enkele zwakke zijdelingse bloeiwijzen vormden.

Het is de vraag of de weinig vertakte, geëtioleerd aandoende habitus van de var. *fontana* in Nederland (Fig. 2) inderdaad steeds het gevolg is van etiolement dan wel (ook) erfelijk bepaald is. Bij herbariummateriaal van buiten Nederland zijn volkomen identieke planten aanwezig en in één geval komt dit uit een Zweeds elzenbosje, Södermanland, 29–6–1927, E. Asplund, Pl. Suecicae exs. ed. E. Hultén [L]. Daarnaast zijn er bij het buitenlandse materiaal ook planten met een gedrongen habitus, waarbij in het geval Ochta (Fig. 3 nr 1) de vindplaats een vochtige weide is, zodat deze planten blijkbaar van onbeschaduwde, althans minder beschaduwde plaatsen afkomstig zijn. Ik had geen gelegenheid zaaiproeven te nemen, die hierover uitsluitsel hadden kunnen geven. Scherp gescheiden taxa zijn het zeker niet, zodat ik ook de gedrongen planten tot hetzelfde taxon reken.

Naar mijne mening blijkt, dat de standplaatsomstandigheden niet de directe oorzaak van het bestaan der taxa zijn; de taxa moeten derhalve een eigen, erfelijk bepaalde plastiek hebben.

De transplantatieproeven werden genomen in het natuur-terrein van Hortus De Wolf (Haren bij Groningen).

Oorzaken van de erfelijk bepaalde plastiek

Knuth (1905) beschouwt *M. fontana* L. als een taxon, dat „zich" op vochtige standplaatsen en door vormreductie heeft onttrokken aan de strijd om het bestaan en daardoor kosmopoliet is geworden. Focke

(1893) vroeg zich af, of de duidelijk succulente habitus van *M. fontana* L. wijst op een afstamming van een woestijnplant, ook omdat onder de Portulacaceae verscheidene xerofyten voorkomen; zie ook ARBER (1920). De eenvoudige bouw van de watervorm van ssp. *rivularis*, waarbij intercellulairen ontbreken, deed GRAEBNER (1895) aan mossen denken. De var. *chondrosperma* beschouwt G. als een jong landtaxon, aangezien deze in bouw van de watervorm slechts verschilt door een dikkere cuticula en kleine intercellulairen. Volgens deze opvattingen staan de erfelijke verschillen op de een of andere wijze in verband met standplaatsinvloeden. Over de reductie van de bloem bij *Montia*, die moeilijk in verband kan worden gebracht met standplaatsinvloeden (het zou kunnen zijn dat groeiplaatsinvloeden een reductie van de vegetatieve organen begunstigden, waarbij de bloemplastiek van dezelfde genen afhankelijk was), zie ALMQUIST (1885) en FRANZ (1908).

Het genoom is onderzocht door HAGERUP (1941), die bij *Montia*-planten uit Denemarken en Zuid-Groenland (hij noemt *M. lamprosperma* CHAM., *M. minor* GMEL. en *M. rivularis* GMEL.) steeds n = 9 chromosomen vond. SCHEERER (1940) heeft echter bij *M. rivularis* GMEL. uit Leer (Oost Friesland, dicht bij het Nederlandse gebied) 2n = 20 chromosomen gevonden, hetgeen HAGERUP (1941) onwaarschijnlijk vindt, daar bij de Portulacaceae steeds het grondtal n = 9 is. H. wijst er op, dat de nauw verwante landplant *Claytonia perfoliata* DONN (syn. *Limnia perfoliata* (DONN) How.) n = 18 chromosomen heeft. De bevindingen van H. wijzen in elk geval niet op diepgaande verschillen tussen onze drie taxa, en steunen de opvatting dat deze tot één soort gebracht moeten worden.

Isolatie van de taxa

Op verschillende vindplaatsen komen de taxa gezamelijk voor, b.v. op natte veengrond var. *chondrosperma* en ssp. *rivularis*, in de beekdalen van Twente var. *fontana* en ssp. *rivularis*. De vraag rijst daarom, hoe blijven de taxa gescheiden?

Men zou bij deze taxa, waarvan de bloemen morphologisch niet of althans weinig verschillen, bastaarden verwachten. Toch komen deze stellig niet algemeen voor, ik ben slechts één geval van een vermoedelijke bastaard tegen gekomen. Bij planten van Ootmarsum, 11–6–1905, P. Jansen en Wachter (*M. minor* Gmel.), L. 924. 33. 155, werd door Kloos in 1946 reeds de aantekening „vermoedelijk een bastaard" gesteld. Het zijn slappe draderige planten, zonder opvallende eindelingse bloeiwijzen, maar toch ook hier en daar met een ongelijk bladpaar onder de top, doch met kleine knobbeltjes op de glanzende zaden. Volgens DELPINO (1900) is *M. fontana* L. uitsluitend autogaam; daardoor zou derhalve bastaarderen slechts bij uitzondering kunnen optreden. Ik kon bij planten van de ssp. *rivularis* in September 1952 waarnemen, dat bij slecht weer de bloemen niet opengingen, maar dat dergelijke bloemen toch normale vruchten en zaden gaven. Deze cleistogamie is reeds lang bekend, cf. KNUTH (1898). Insectenbezoek heb ik bij de *Montia*-planten in het Drentse flora-district nimmer waargenomen.

SUMMARY

Montia fontana L. in the Netherlands

The literature on *Montia fontana* L. in the Netherlands was reviewed and discussed (part 1). The nomenclature of the taxa was discussed and correct names were established (part 2). A taxonomy was given (part 3). The plastics of the taxa was described and discussed, whereby the results of some transplantation experiments were considered (part 4).

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ON THE IDEAL VALUE OF VARYING CHARACTERS

BY

J. G. MEIJKNECHT o.e.s.a.

(Eindhoven)

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I. INTRODUCTION

It is a well-known fact that the leaves of each plant, and also several of its other parts, show such a wide range of diversity, that it is hardly possible to find two corresponding ones that may be regarded as fully identical.

Yet, even a superficial examination of the leaves, to confine ourselves to the latter, leads to the conclusion that, notwithstanding the enormous variability of their characters, they belong in each species to a definite type; this type is, in most cases, characteristic for particular species.

It is but natural that we should try to find a method by the aid of which this type may be recognized in the midst of this, at first sight, rather chaotic diversity. When, by the aid of this method, we have found this type, we will try to express it in a mathematical form. The linnean terminology appears to be insufficient for our purpose. Terms like: "oval, oblong, lobed, split, etc." are not sufficiently precise to deal with the numerous gradations with which we are confronted.

It is a thing of common experience that, how variable a character may be, its average value is met with, as a rule, most frequently, and is therefore its most familiar expression. Even without exact measurements, i.e. simply by direct observation, this average is therefore usually recognizable, though more or less vaguely.

In fact, it is on the ground of this experience that the characters of a species are defined, for this definition rests on the belief, that the value that is most often met with, is representative for the species.

It is therefore a matter of course that average values are regarded as expressing certain predispositions, which are to be taken as the elements of a specific constitution.

It will be obvious, that in looking for a value that can be accepted as representative of a character in a definite species, which value we will call "the ideal value", we will have to turn our attention to the average values that are found by measuring groups of specimens. However, in order to obtain serviceable averages, it appeared to be necessary to take into account what position the parts of which the characters are studied, occupy in the general plan on which the plant is built.

When we calculated the averages of groups of measurements obtained from leaves occupying corresponding positions on the shoot, we found not only some very satisfactory values but also surprising rules. For this reason we have in the following study always compared leaves which occupy a corresponding position on the shoot. As our investigations went on, we did not confine ourselves to the leaf size, but we studied also other features that are to be observed in the leaf, as the size of the angles between various nerves and the relative length of the petiole and blade: characters of other parts of the plants too were dealt with in the same manner.

It is therefore of primary importance to arrange the parts into natural groups based on the position they occupy in the general plan of the plant: the determination of the average and of the ideal value of a character is then merely a question of measuring and calculating. Only by applying this method it appeared possible to reach our aim, viz. to find for each character the value which we regard as the ideal one.

That often a distinct relation was found between the degree of development of an organ and the position it occupies in the general plan of the organism, is not the only point that deserves our attention. An other point is that the degree of variability too proves to depend upon the position the part occupies in the organism. However, the quantitative and qualitative differences in the variability of these parts has never yet been studied with statistical methods.

This study has taught us, that it is unpractical to calculate averages from quite arbitrarely chosen material, but that the parts that are to be measured should be assembled in groups according to their morphological character, which is determined by the position they occupy in the general plan of the organism: this must be the guiding principle in statistical studies of this kind.

At first view it will perhaps seem strange that this study has not been carried out with clones or pure lines or at least with material of which the genetical constitution is more or less known.

However it should be realized that the most important aim of this study is to obtain some insight into the nature of characters as they appear in species that are met with in nature. We have tried to attain this aim by studying plants of which, on the ground of certain distinctive characters, we were convinced that they belong to a definite species.

The material has therefore, as a rule, been collected from several specifically identical plants; when it has been taken from a single plant this will always be definitely stated.

The choice of the plant species for this study was determined only by the circumstance that these plants were easily at hand: the characters were chosen in such a way that they were as different as possible and that they were easily measurable.

The method described above has not only been applied to the material that we ourselves have collected and measured but also to some series of measurements found in the literature. In this way we wished to test the validity of the rules which had been found in the study of our own material for characters that we ourselves did not investigate. The study was extended to the following characters and species:

Own investigations:

A. Ratio between the length of various nerves in
  a. *Acer palmatum* var. *septemlobum.*
  b. *Acer cappadocicum.*
  c. *Platanus acerifolia.*
  d. *Batrachium fluitans.*

B. Size of the angle between various nerves in
  a. *Acer cappadocicum.*
  b. *Platanus acerifolia.*

C. Ratio between the length of various nerves as well as size of the angle between the nerves in
  Tropaeolum lobbianum.

D. Length of the leaf blade in
  a. *Acer palmatum* var. *septemlobum.*
  b. *Acer cappadocicum.*
  c. *Platanus acerifolia.*

E. Ratio between the length of petiole and blade in
  a. *Acer platanoides.*
  b. *Acer pseudoplatanus.*
  c. *Batrachium fluitans.*

F. Relative leaf width in
  Ligustrum ovalifolium.

G. Number of umbel rays in
  Aegopodium podagraria.

Testing of the rules found in our own material on data obtained from other investigators: these data regarded:

A. The size of the meshes between the reticulated veins in the leaf of
  Vitis vulpina.

B. The relative length of the internodia in

Fagus sylvatica.

C. The ratio between the number of stomata and the number of epidermis cells in

Teucrium chamaedrys.

Acknowledgements

At the completion of this study I wish to express my sincere thanks in the first place to Prof. Dr. C. E. B. Bremekamp (Utrecht) for his valuable advices, his interest in my work and his correction of the English text.

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II. OWN INVESTIGATIONS AND THE RULES DERIVED FROM THEM

A. Ratio between the length of different main nerves in the same leaf

In opposition to Goebel (1922) Uittien (1928) was of opinion that the morphological character of a leaf is determined mainly by its venation and not by its outline. He expressed this view in the following way: "It is clear that morphologically it is not the outline but the venation which is of greater importance".

We fully agree with this opinion, for the outline of a leaf is, as this study has shown, primarily determined by the relative length of the nerves and by the size of the angle between them.

Several investigators have tried to detect a regularity in the varying leaf forms. However, by neglecting the structural importance of the nerves and by confining their attention to the outline of the leaf, they remained literally and figuratively on the outline of this problem.

Shull (1905) arranged the leaf forms of *Sium cicutifolium* according to the sequence in which they appear on the stem, and he came to the conclusion that the most extreme forms are met with in the lower leaves, whereas the variability reaches its lowest value in the upper leaves of the stem. But he only paid attention to the outline of the leaf and he did not at all consider the venation. By this oversight the building plan of the leaf, on which all the varying forms are founded, remained hidden to him.

The same applies to the study which Hammond (1941) made of the variability in *Gossypium.*

SMIRNOV and ZHELOCHOVTSEV (1931) too failed to recognize the structural importance of the venation when they studied the venation of the leaf form in *Tropaeolum majus*. Aside from the fact that they wrongly interpreted the changes in the outline of the growing leaf as conchoidal, they mistakenly regarded the leaf as built up of a number of fields that each are enclosed by two of the main nerves. However it is much more plausible to regard this leaf as composed of fields that are equally developped on both sides of a main nerve; this means that the part enclosed between two main nerves can structurally not be considered as an entity, but forms a combination of two half fields; therefore, as their calculations are based on a view which disregards the real structure of the leaf, their value is to be considered as highly doubtfull. AHSBY (1948) ironically remarks: "This is a somewhat Procrustean treatment of the data" (p. 157.), and this seems hit the mark.

A similar objection can be made against THOMPSON (1917) who in discussing the leaf form divides the leaf in sections by arbitrary lines, which intersect the venation. He bases his conclusions regarding the development of the leaf on the changes which these arbitrary sections undergo, disregarding the fact that the leaf form is determined mainly by the venation.

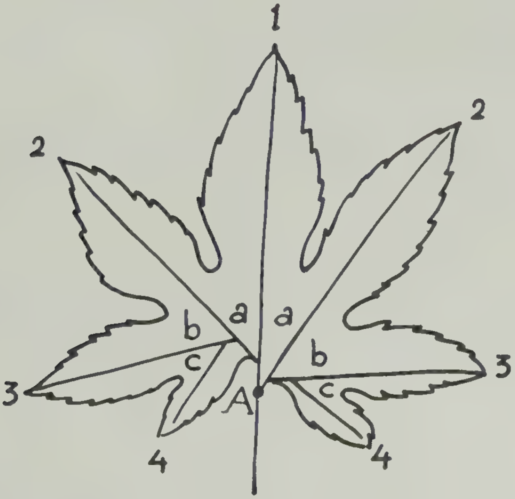

Fig. 1. Indication of the nerves and of the angles between the nerves in a palmatifid leaf. (*Acer palmatum* var. *septemlobum*)

In the conviction that the venation is of primary importance for the form of the leaf, our investigations were in the first place directed to the ratio between the length of the various nerves in several plant species: our principal aim was to find for each plant species a constant value for this ratio.

a. Ratio between the length of the main nerves in the leaf of *Acer palmatum* var. *septemlobum*

The length of the nine main nerves was determined in some hundreds of leaves of this type. The leaves were arranged in groups in according to the position they occupied on the shoot: the nerves were numbered as indicated in Fig. 1.

Further, the length of the nerves 2, 3, and 4 is expressed in percents of that of nerve 1. For this purpose we always took the average length of the two corresponding nerves in the right and in the left half of the leaf.

In this study the sequence in which the leaves are inserted on the shoot is always taken in consideration: the lowest leaf or leaf pair of each shoot is in this study always indicated by the letter "A"; the following one by "B", etc.

When we speak of a higher leaf we always mean a leaf that is inserted higher on the shoot. The word "higher" does not mean that the leaf to which it is applied, is "higher" developed or shows a higher ratio between the length of the lateral main nerves and the central one. As we will see in the course of this study there is in this respect a striking contrast between the leaves of the *Acer* and *Platanus* species.

From leaf class "A" 200 leaves were measured, and these were classified according to their size in 4 groups of 50 leaves: apart from these we measured 50 leaves of each of the leaf classes B, C, E and G, selecting the largest ones, and of the leaf class F 50 leaves of the smallest and 50 leaves of the largest size.

The average length of the nerves 2, 3 and 4 expressed as a percentage of that of nerve 1 was calculated for each group of leaves and these values are given in Table I.

TABLE I

Relative length of the lateral main nerves in the leaves of *Acer palm. sept.*

Position of the leaf	Size group	Number of leaves per group	Aver. length nerve 1 in mm	Aver. length in per cents of nerve 1		
				Nerve 2	Nerve 3	Nerve 4
A	I	50	33	90	65	35
	II	50	42	91	67	38
	III	50	50	91	68	39
	IV	50	56	92	69	40
B		50	48	84	45	19
C		50	52	85	52	19
E		50	45	86	41	19
F	I	50	34	73	38	—
	II	50	49	79	41	—
G		50	39	71	37	—

In considering these results one has to distinguish between ontogenetic development (the growth of a leaf from its first appearance until it has reached its ultimate size: compare the 4 size groups of leaf class A) and the morphological differentiation. In order to obtain an insight in the latter we should compare the final stage of leaves inserted in different positions on the shoot; viz. the largest leaves of classes A to G. Among the leaves of class A the 50 of size group I remained rather small. We may safely assume that these leaves would have grown no more as they were collected towards the end of the summer, i.e. at a time when all normal leaves are since long full-grown.

The size group II and III form gradual transitions to size group IV: the 50 leaves of these size groups were (nearly) full-grown, not alone ontogenetically but also morphologically: this means that they had attained the highest stage of development that a leaf in the position A can attain.

When we compare the 4 size groups of leaf class A we notice a slight increase for each nerve. The smallest value is found for nerve 2. The maximum is reached in group IV, viz. for nerve 2: 92 %, for nerve 3: 69 %, for nerve 4: 40 %.

This rather striking constancy in the nerve length ratio appears already when the leaves are studied in the bud. To this end the relative nerve lengths of leaves of class A were determined with the aid of a drawing prism: in these leaves the length of nerve 1 proved to vary from 470 μ to 950 μ. The average nerve length ratio was here for nerve 2: 94 %, for nerve 3: 65 % and for nerve 4: 32 % (Table II).

TABLE II

Relative length of the lateral main nerves in leaves of class A in buds of *Acer palm.* var. *sept.*

Number of leaves	Aver. length nerve 1 in μ.	Aver. length in per cents of nerve 1		
		Nerve 2	Nerve 3	Nerve 4
10	474	94	66	31
10	558	96	69	36
10	626	95	67	34
10	744	93	60	27
10	904	90	65	34
Aver. 50	661	93,6	65,4	32,4

Comparison of these figures with those of Table 1 shows that the relative length of the nerves 2 and 3 has already attained its final value when the leaf has reached a length of circ. 0,5 mm, but that the relative length of nerve 4 increases considerably during the growth of the leaf.

It is rather difficult to recognize in these leaf primordia the point where the nerves begin, but in view of the quite satisfactory agreement between the figures, the values given in Table II impress us as trustworthy.

From these data the conclusion may be drawn that the form of the leaf in this *Acer* species undergoes little or no change during its ontogenetic development.

The question whether it is admissible, as we have done here, to conclude from differences in the averages found for small and large leaves to a change in the form of "the" leaf of a species, will be discussed furtheron (p. 296).

When we compare ontogenetically full-grown specimens belonging to the leaf classes A to G it appears that the averages of the nerve length ratio show a considerable decrease; the value for nerve 2 has decreased with ± 1/5; that for nerve 3 with ± 1/2: and nerve 4 becomes so short that it is in the higher leaves no longer accurately measurable.

The average nerve length ratio reaches its highest value in the full-grown leaf of class A. This leaf type shows the highest possible degree of development in the ontogenetic as well as in the morphological sense.

We can recognize a series of morphological stages which have their climax in the leaf class A and show from there to leaf class G a gradual decline; in leaf G appears an anti-climax. This decline from base to top can be called "kathodic".

We will see furtheron that in some other plant species it is on the contrary leaf class A in which the lowest figures are found for the average nerve length ratio, whereas the highest values are reached in the higher leaves; for such an ascending morphological series we will use the term "anodic".[1]

Estimation of the measuring errors

Unavoidable errors are made in all our measurements. In the first place in determining the place of origin of the nerves we often make an error of 1 or 2 mm. Moreover the origin of nerve 2 is very often higher at one side of the leaf than at the other. In order to follow everywhere the same line of conduct we have always taken the point where the lower nerve 2 branches off from nerve 1 as the point of origin (point A in Fig. 1).

In addition to this the nerves, especially in full-grown leaves, are very often slightly bent; this always caused a measuring error of some mm. In leaves of 100 mm or more an error of 1 or 2 mm has little importance: however in leaves that are smaller than 20 mm it reaches a value of 5 % or more.

Nevertheless it is not reasonable to suppose that these errors in the hundreds of measurements should all have been made in the same direction. In such large numbers of measurements the positive errors will be compensated by the negative ones. Therefore it seems admissable to assume that the enevitable measuring errors not have had an influence of importance in our calculations of the average.

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[1] These terms are taken from a quotation of Heraclitus (fragm. 76. Diels.) „*μεταβολὴν ὁρᾷς σωμάτων καὶ γενεσεωσ ἀλλαγην, ὁδον ἀνω καὶ κατω.*" "You see changes of bodies and reversal of genesis — a way upwards and downwards". I owe these terms to H. Höppener, litt. class. dr. (Eindhoven): they express the idea very adequately.

Standard deviation and variation coefficient

All the foregoing conclusions have been based on averages calculated from a number of percentages, i.e. of a number of variates. In order to estimate the magnitude of this variation (the variation width) the standard deviation of these averages was calculated by means of the usual formula $\mathrm{S\,D} = \pm \sqrt{\frac{\Sigma^n (x_i - \bar{x})^2}{n(n-1)}}$.

x_i is the value found as average of all the variates and $\bar{x}$ is the value of the individual variate: n is the number of variates. The values found for the S D of the nerve length ratio in the various groups were not directly comparable, for when we find for the S D e.g. a value of 0,5, it makes a great difference whether the relative nerve length is 90 % or whether the latter is 30 %: in the last case the relative importance of the S D is thrice greater than in the first case.

In order to obtain comparable figures we have calculated each time the relative value of the S D, i.e. the value that is known as the variation coëfficient (V C) and that is calculated by means of the formula $\mathrm{V\,C} = \frac{100 \times \mathrm{S\,D}}{\text{average}}$.

In the further course of this study we will give the V C for each average as this is a useful measure of the variation width.

However in comparing the values found for the V C it should be born in mind that this should be based on the same number of variates: the value of the S D, and therefore that of the V C too, depends partly on the number of variates. For the magnitude of the numerator in the formula of the S D depends on n and that of the nominator on the *square* of n, or to be more exact, on $n(n—1)$.

With an increase of n the denominator increases more rapidly than the numerator, with the result that the S D and the V C decrease. In order to obtain comparable values for the V C it is necessary that the groups consist as much as possible of an equal number of leaves. However, when it was impossible to work with groups consisting of an equal number of variates, the following method was applied.

Assuming that the S D of a group of 50 variates was to be compared with that of a group of 100 variates the value obtained in the latter case for the numerator was divided by $\frac{100}{50} = 2$, whereas that of the denominator was divided by $\frac{100 \times 99}{50 \times 49} = 4{,}041$: from the figure that was obtained in this way the square root would have to be taken. In our example this means that the value calculated for the V C of 100 leaves is to be multiplied by $\sqrt{2.02}$, or roughly by 1,4. In our opinion this is a fully justified procedure when the V C of groups consisting of an inequal number of variates are to be compared.

In Table III the values found in *Acer palmatum* var. *septemlobum* for the S D and the V C of the average nerve length ratio in the leaf classes A and F are given. It appears from this table that the V C decreases when

1) the leaf approaches the end of its ontogenetic development, i.e.

when it reaches its largest size (compare the value found for the nerve length ratio in the different leaf size groups belonging to the two leaf classes)

2) we proceed to the leaf that belongs to the class in which the highest average values are found (compare the leaf classes A and F)

3) when we proceed to the nerve length ratio which shows the highest average value (compare the nerve length ratio for the nerves 2 and 3).

TABLE III

Values found in *Acer palm. sept.* for S D and V C of the average nerve length ratio in leaves belonging to the classes A and F.

Position of the leaf	Number of leaves in size groups	Aver. length nerve 1 in mm	Value of S D						Value of V C		
			Nerve 2 %	Nerve 2 S D	Nerve 3 %	Nerve 3 S D	Nerve 4 %	Nerve 4 S D	Nerve 2	Nerve 3	Nerve 4
A	50	0,66	94	0,81	65	1,23	32	1,10	0,87	1,90	3,40
	50	33	90	0,64	65	0,84	35	0,84	0,71	1,26	2,40
	50	42	91	0,53	67	0,80	38	1,20	0,58	1,22	3,20
	50	50	91	0,55	68	0,53	39	0,73	0,60	0,77	1,90
	50	56	92	0,38	69	0,42	40	0,53	0,41	0,62	1,31
F	50	34	73	1,20	38	0,58			1,60	1,55	
	50	49	79	0,77	41	0,35			0,98	2,08	

Summarizing we may say that the lowest V C of the nerve length ratio was found in the nerve that shows the highest degree of development in an ontogenetic as well as in a morphological sense: in this species it is nerve 2 in full-grown leaves of class A.

The figures given in this table also show that the V C decreases as the average approaches its highest value.

It is of little or no importance that in the regularity with which the series of V C's decreases occasionally a small irregularity occurs (nerves 3 and 4). The absolute figures are not so much of importance as their decrease or increase, and as the place where the lowest value of the V C is found.

The high figure of the V C indicates a high degree of variability in the length of the nerves 3 and 4, but when among such a relatively small number of variates extreme plus- or minus-values occur, the V C will attain even a higher value than one would have expected. However, the general trend of the descending course of the V C parallel to the increase of the average nerve length ratio is not obscured by such occasional irregularities.

The final aim of this study is to determine the optimum degree of development and the value shown by the V C at that stage. It is of little importance to determine the value of the V C's for all those groups of leaves which do not show the optimum degree of development: it will be sufficient to show that they have a higher V C, and it does not matter how high the latter precisely is. The lowest V C is a diagnostic criterium, and perhaps the most important one, by which the optimal degree of development can be recognized.

A more precise definition of the optimum degree of development

The results of certain studies, which will be communicated further on, raised the question whether the degree of development of the shoot as expressed in the number of leaf pairs, might perhaps have some influence upon the development of the nerves and on their variability, i.e. on the nerve length ratio and its V C.

The leaves of this species grow always in pairs and the number of leaf pairs on each shoot proves to vary considerably. There are shoots with 1, 2, 3, 4 or even more than 6 of leaf pairs. In order to find out whether there is some relation between the nerve length ratio and the number of leaf pairs per shoot, we have calculated the average of nerve length ratio for the nerves 2, 3 and 4 in 6 groups each consisting of 100 leaves belonging to class A as they occur in shoots with respectively 1, 2, 3, 4, and more than 6 leaf pairs (Table IV).

TABLE IV

Average nerve length ratio with its V C in leaves of *Acer palm.* var. *sept.* belonging to class A and inserted on shoots with 1, 2, 3, 4 and > 6 leaf pairs.

Number of leaf pairs on the shoot	Number of leaf pairs per group	Nerve 1		Nerve 2		Nerve 3		Nerve 4	
		in mm	V C	%	V C	%	V C	%	V C
1	100	45	1,4	89,7	0,32	66,0	0,67	36,6	0,95
2	100	45	0.96	91,4	0,36	70,0	0,73	40,0	1,10
3	100	50	0,68	92,1	0,30	72,4	0,53	40,8	0,90
	100	48	0,71	91,9	0,30	70,6	0,40	39,7	0,88
	200	49	*0,70	92	*0,30	71,5	*0,46	40,2	*0,89
4	100	50	0,74	92,2	0,38	70,7	0,60	38,2	0,97
>6	100	53	1,13	93,5	0,34	73,7	0,66	41,8	1,50

* V C, if necessary adjusted to a basic number of 100 variates.

It appears from the figures of this Table that the average length of the nerve 1 as well as the average nerve length ratio for the nerves 2, 3, and 4 increase with the number of leaf pairs per shoot.

However, if we look at the figures of the V C than it appears that the leaves of shoots with 3 leaf pairs show the lowest V C : as a control a second group of 100 leaves was studied.

The figures for the average length of nerve 1 as well as those for the nerve length ratio for the nerves 2, 3 and 4 and those for the V C show in these two groups of 100 leaves, especially for nerve 2 and 4, a very good agreement. This strongly corroborates our supposition that these figures may be considered as a trustworthy reflection of a natural relation: that the variation width has reached here its lowest value demonstrates that the leaf shape approaches here its ideal value.

In our first set of investigations we found that the variability of a character decreases as the latter approaches ontogenetically and morphologically its final value. Therefore we concluded that the variation width is a criterium for the rate of development in this sense that a lower degree of variability corresponds to a higher degree of development. The nerve length ratio of the leaves belonging to class A and produced by shoots with more than 6 leaf pairs shows indeed the highest value, but their variability is greater than that found in leaves of shoots with 3 leaf pairs.

However, when we stick to the rule that the ideal value always goes with the lowest width of variation, we come to the conclusion that the nearest approach to the ideal value is found in the leaves produced at the base of shoots with 3 leaf pairs.

We prefer the latter solution and we disengage ourselves therefore from the idea that the highest value of a character is identical with or the nearest approach to the ideal degree of development, i.e. to the degree of development which best expresses the nature of the species.

Although we originally (p. 282) formulated our conclusion in this way that the lowest degree of variability is a criterium, and perhaps the most important one, of the highest average value that a character may reach, it now appears more appropriate to express it in the following way: *the lowest degree of variability (V C) is pre-eminently the criterium of the ideal value of a character.*

Therefore, we come to the conclusion that the ideal value of the nerve length ratio in the leaves of *Acer palmatum* var. *septemlobum* is that which is exhibited by the leaves of class A in shoots with 3 leaf pairs, and that it comes for nerve 2 to 92 %: for nerve 3 to 71,5 %: for nerve 4 to 40,2 %.

The predisposition

From the data of Table I it appears that the leaves that occupy corresponding positions on the shoot form groups in which the nerve length ratio oscillates round a definite average. In each leaf and for each character of the latter a predisposition must be accepted that is determined by the position of the leaf; a local predisposition, therefore, that finds its expression in the figure of the average. In leaf groups that occupy different positions the local predispositions are different; in each of them the characters show their own average.

As the nerve length ratio of individual leaves occupying corresponding positions on the shoot and belonging, therefore, to the same group may deviate rather far from the average, and as the average value found in groups consisting of leaves, that occupy a different position, may sometimes be very close to each other, it is evident that repeatedly leaves will be found with the same nerve length ratio and which nevertheless belong to different groups. These leaves show the same phaenotype but possess a different predisposition.

It is possible to construct a continuous series of values for the nerve length ratio descending from the most extreme plus-variate in a leaf belonging to class A to the most extreme minus-variate in a leaf belonging to class G (or perhaps to class H or I.)—a complete series of gradual transitions from the highest to the lowest value.

Because of this series of transitions UITTIEN (1939) regards it as impossible to express a specific character in a figure. He says: "It is impossible to express in figures the number of types, for there are complete series of transitions. Reference to a definite type is a question of judgement, that is to say, it is necessarily subjective. This entirely deprives the statistical method of its value." (p. 468).

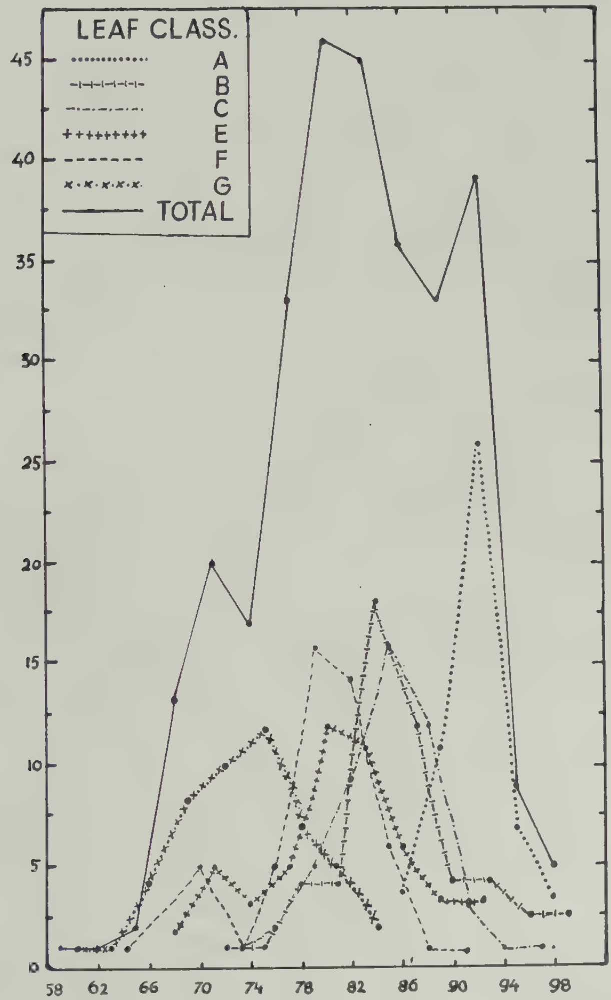

Fig. 2. Nerve length ratio for nerve 2 in per cents measured in groups at 50 leaves belonging to the classes A, B, C, E, F and G and in all these leaves together.
Horizontal: Value of the nerve length ratio in per cents.
Vertical : number of leaves in the various classes. (*Acer palmatum* var. *septemlobum*)

The preceding exposition definitely shows that this is an underestimation of the value of the statistical method and, therefore, unacceptable. Indeed, when we collect indiscriminately leaves that occupy different positions on the shoot, than, as we will demonstrate now, it will be impossible to find a significant average.

In order to find out what the result would have been when leaves that occupy different positions on the shoot should have been collected (this is how UITTIEN thought that the statistician would obtain his material), we have separately plotted in curves the figures of the nerve length ratio found for nerve 2 in 6 groups each consisting of 50 leaves that respectively belonged to the classes A, B, C, E, F and G (the averages calculated for these groups have been given in Table I), and in addition to these 6 curves we have given a curve comprising all these 300 leaves: in this last-named curve, therefore, the leaves belonging to the classes A, B, C, E ,F and G have all been brought together so that the significance of the position they occupy on the shoot has been obliterated (Fig. 2).

We see in this graph that the 6 curves representing leaves belonging to different classes have each but a single top, and that the top of the curve which represent the leaves belonging to class A attains the highest level. The curve that represents the whole lot, on the contrary, shows more tops, and is very irregular. This irregularity is all the more significant as this curve is based on a larger number of leaves, so that we might have expected a greater regularity.

This clearly demonstrates that the curve representing the 300 leaves cannot be regarded as the expression of a homogeneous material, and that its average, therefore, is not to be taken as expressing a definite predisposition: the whole group might be compared to a population, whereas the 6 classes of leaves A to G have the character of pure lines.

The arrangement of the leaves in groups is not arbitrary but was based on our conviction that the leaves possess a certain predisposition that is determined by the position they occupy on the shoot.

It is, of course, impossible to observe this predisposition directly, but this applies to every predisposition. What we observe are differences between the various specimens, in which each time one of the possibilities is realized, but in order to recognize the predisposition it is necessary to apply the described method.

Our final conclusion is that for characters such as the nerve length ratio a definite predisposition is present, which finds its expression in the ideal value and can be expressed in a figure.

b) *The nerve length ratio in leaves of Acer cappadocicum Gled.*

In order to find out whether the rules which were derived from the data given in the foregoing study have a general validity, the nerve length ratio was studied in the same manner in the leaves of another *Acer* species.

The leaves of this species possess, no matter what position they occupy on the shoot, but 5 clearly recognizable main nerves: the number of the leaf pairs in each shoot is also more limited: leaves of class E are found but seldom.

For a first orientation, i.e. without paying attention to the number of leaf pairs in each shoot, the average nerve length ratio was calculated for two groups of 50 leaves belonging respectively to the classes A and C (Table V).

TABLE V

Nerve length ratio in the leaves of *Acer cappadocicum*.

Position of the leaf	Number of leaves	Aver. length of nerve 1 in mm.	Aver. nerve length ratio in per cents of nerve 1	
			Nerve 2	Nerve 3
A	50	85	92,6	66,8
C	50	65	86,6	55,4

The figures for the average nerve length ratio form just as in the leaves of *Acer palm. sept.* a kathodic series, i.e. the highest average is found in the leaves of class A.

To determine this highest average with greater precision the average nerve length ratio was calculated in 3 groups each of 100 leaves belonging to class A in shoots with resp. 2, 3, and 4 leaf pairs (Table VI).

TABLE VI

Nerve length ratio in leaves belonging to class A in shoots with 2, 3 and 4 leaf pairs of *Acer cappadocicum*

Number of leaf pairs in the shoots	Number of leaves	Average length Nerve 1		Average nerve length ratio			
				Nerve 2		Nerve 3	
		in mm	V C	%	V C	%	V C
2	100	67	2,20	91,3	0,32	69,0	0,88
3	100	80	0,66	92,7	0,27	69,9	0,54
4	100	83	1,07	92,7	0,30	67,7	0,67

The leaves on the shoots with 1 leaf pair are so small that one can say beforehand that the highest value will not be found here, and for this reason they were discarded.

In this species too the leaves of shoots with 3 leaf pairs show not only the highest average nerve length ratio for nerve 2 as well as for nerve 3, but also the lowest V C. Here, therefore, the ideal value of the nerve length ratio is found, and it amounts for this species for nerve 2 to 92,7 % and for nerve 3 to 69,9 %.

Both *Acer* species show, therefore, a striking resemblance in the position of the leaves with the ideal value, as the highest average as well as the lowest V C are found in the same leaf class. The average nerve length ratio is different for each species, and this value is, therefore, to be taken as characteristic for the species.

c) *Nerve length ratio in the leaves of Platanus acerifolia W.*

At first view it seems that the leaves of this species are very different in form according to the position they occupy at the shoot: most of the leaves belonging to class A are more or less elliptic or ovate, whereas the higher leaves become more and more distinctly palmatifid.

This difference is however more apparent than real, for at a closer examination it appears that in most cases the leaves belonging to class A have a distinctly palmate venation. However, as the nerves are here as yet ill-developed and as the angles between the nerves are small, in most cases the outline of these leaves is unbroken and forms a nearly perfect oval.

Here Uittien's idea, that the venation is of primary importance for the leaf form comes to full play; it offers us here a means to reduce all the leaves of this species to the same ground plan, no matter what their outline may be; they are all palmately nerved. In measuring the nerves of this species the same difficulties occur as in the leaves of the *Aceraceae* and they have been solved in the same manner.

The value of the average nerve length ration and of the latter's V C for leaves occupying successive positions on the shoots are given in Table VII.

TABLE VII

Nerve length ratio and V C in the leaves of *Platanus acerifolia*

Position of the leaf	Number of leaves	Length nerve 1 in mm	Nerve length ratio			
			Nerve 2		Nerve 3	
			%	V C	%	V C
A	100	18–36	75	1,53		
	100	36–46	73	1,18		
	100	70–83	72	1,23	48	3,19
	100	82–125	76	1,05	50	2,35
E	100	18–100	84	0,47		
	100	160–250	82	0,38		
G	100	110–165	85	0,52	65	0,77
	100	165–210	83	0,37	64	0,64
I	100	140–175	85	0,45	65	0,65
	100	175–220	83	0,38	66	0,56

A comparison of these figures shows that the average nerve length ratio for the nerves 2 and 3 as determined for leaves occupying a definite position on the shoot remains practically the same, no matter to which size group the leaves belong; differences of 1 or 2 % are negligeable.

The form of the leaves undergoes little or no change during the ontogenetic development.

When we compare the full-grown leaves occupying different positions on the shoot, we notice a clear contrast between this species and the *Aceraceae* studied above: the average nerve length ratio shows here the lowest value in leaf class A, whereas the highest value is attained in leaves that occupy a higher position on the shoot; the successive values for the average show in this species an "anodic" series.

We see in the ontogenetic development of the leaves (compare the smallest and the largest leaves occupying corresponding positions on the shoot) and also as we proceed to higher stages in the morphological series (compare the full-grown leaves occupying successive positions on the shoot, from leaves belonging to the class A to those belonging to the class G (or, eventually, I) a decrease of the V C which reaches its lowest value in leaves belonging to class G.

To determine the highest average value for this species with greater precision the values for the average nerve length ratio and their V C were calculated, first for 100 leaves belonging to class E on shoots with a leaf E as top leaf, and next for 100 leaves belonging to the same class in shoots with leaf G (or a leaf belonging to a higher class) as top leaf.

Furthermore 100 leaves belonging to class G were measured in shoots with a leaf G as top leaf and twice 100 leaves of class G in shoots with a leaf I (or a higher leaf) as top leaf. Finally 100 leaves of class I were measured in shoots with leaf I (or a higher leaf) as top leaf (Table VIII).

TABLE VIII

Nerve length ratio and V C in definite leaves of *Platanus acerifolia* in shoots with a different number of leaves.

Position of the leaves	Class to which the top leaf of the shoot belongs	Number of leaves	Nerve 1		Nerve 2		Nerve 3	
			in mm	V C	%	V C	%	V C
E	E	100	160	0,90	82	0,46	59	1,0
	>G	100	175	0,78	83,5	0,39	62	0,92
G	G	100	160	1,25	83,3	0,40	63	0,75
	>I	100	181	0,80	83,0	0,38	63	0,60
		100	171	0,70	83,6	0,37	63,8	0,56
I	I	100	146	1,45	83,4	0,48	62,7	0,61

From these figures it appears that in the leaves belonging to class E the average nerve length ratio shows a slight increase when the number of leaves on the shoot increases: this increase is accompanied by a diminution of the V C.

The average nerve length ratio in the leaves G show the same value: the V C reaches its lowest value in the shoots with the largest number of leaves. To check the results we have calculated the average values and their V C for two groups of 100 leaves of this last class. The figures obtained for these two groups show a striking similarity, those for the averages as well as those for the V C. The leaves of class I show nearly the same average values as the leaves of class G, but their V C is higher. This last fact indicates that we cannot regard these leaves as the ideal ones. On the ground of the value of the V C we must accept the value found for the leaves of the class G as the ideal one; it amounts for nerve 2 to 83,3 % and for nerve 3 to 63,4 %.

It is not excluded that the degree of development of the tree has some influence on this ideal value: the V C might be lower in trees which have attained the fullest development. In trees which were in the period of their greatest vigour much more shoots with a larger number of leaves were noted than on trees which already had reached their ultimate height, which were, so to speak, in the autumn of their life.

It is not to be expected that the oldest trees will show the ideal value, no more than that the ideal value of the nerve length ratio is found in the leaves of class I.

However, as no sufficient trees of different age were found in our neighbourhood, we could not study this question.

d) *Nerve length ratio in the leaves of Batrachium fluitans Lam.*

This waterplant has stems with a length of 3–4 m and with up to 25 alternate leaves. The submerged leaves consist of the nerves only: there is practically no mesophyll. We never found floating leaves: they are in this species extremely rare.

It is very difficult, and sometimes even impossible, to determine the exact position of the leaves on the shoots, for it is often excluded to determine with some degree of accuracy which leaves belong to "leaf class A".

The stems of these plants are rooting on the lower nodes, and they are in this manner attached to the sandy bottom of the little streams in which they occur. It often happens that leaves are found at the first nodes above the bottom, but sometimes they do not occur below the third node. In such cases it is impossible to decide whether the leaves at the foregoing nodes have already disappeared, as the first leaves die early in the year.

Because of this uncertainty a margin of 2 or 3 leaves should always be allowed in determining the position. For this reason the leaves were arranged in 5 groups: the 100 leaves of each group belong to at least 3 successive classes, viz.

Group	I	comprising	leaf	classes	A, B, C.
„	II	„	„	„	D, E, F.
„	III	„	„	„	G, H, I.
„	IV	„	„	„	J, K, L.
„	V	„	„	„	M–W.

Each leaf is composed of 3 main nerves: the central one is small and thin (nerve 1); the 2 other ones are longer and thicker (nerve 2) (Fig. 3).

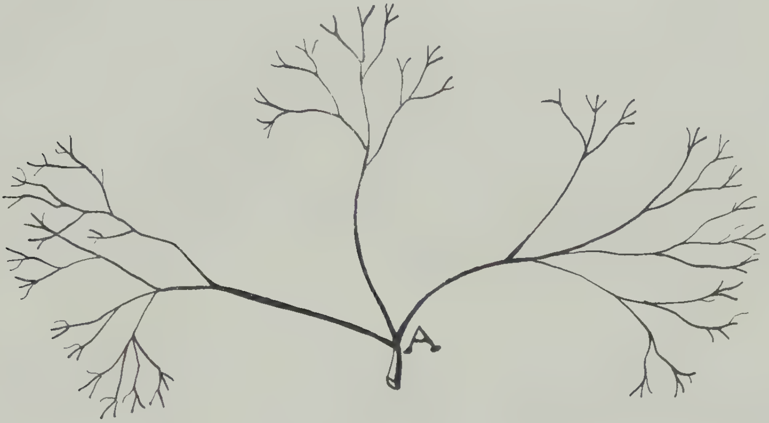

Fig. 3. Leaf of *Batrachium fluitans*. (A: point of origin of the nerves.)

When the leaves are taken from the water for measuring, the ramifications of the 3 main nerves fall together in the form of a brush.

In order to measure the length of the nerves the point A, where the 3 main nerves separate, is always taken as the beginning of the nerves and the brush at the top as the end.

The average nerve length ratio for the 50 smallest and for the 50 largest leaves of each group and their V C is given in Table IX. It appears from this table that nerve 1 attains its greatest length in group III, and that there is but little difference between the average nerve length ratio of the 50 smallest and of the 50 largest leaves of each group.

TABLE IX

Nerve length ratio and V C in leaves of *Batrachium fluitans*

Group	Position of the leaves	Number of leaves	Length of nerve 1 in mm	Nerve 2	
				%	V C
I	A.B.C.	50	41–92	123	1,42
		50	130–192	120	1,38
II	D.E.F.	50	41–95	126	1,38
		50	171–216	119	1,08
III	G.H.I.	50	49–142	123	1,69
		50	175–241	120	1,18
IV	J.K.L.	50	44–139	118	1,38
		50	172–233	119	1,02
V	M.–W.	50	20–107	111	1,43
		50	129–216	118	1,02

Comparison of the largest leaves too fails to reveal a marked difference. We can determine therefore the nerve length ratio for all leaves at 119 %.

In each group the average of the 50 largest leaves shows a lower V C and in groups IV and V the V C is the lowest of all. It should be realized that group V comprises the 14-th to the 24-th leaf on the shoot, and this corroborates our opinion that the ideal value of the nerve length ratio is to be found here. We can accept in the leaves of this species on account of the figures for the V C an anodic series.

Sufficient material was collected (it is not of importance for the present to determine the ideal value more precisely) to yield a basis for comparing the variability of the leaf blade with that of the petiole, which will be discussed furtheron.

II. B. The size of the angle between the nerves

The size of the angle between the nerves of the leaves has also been subjected to a statistical investigation in order to find out whether the rules which pertain to the nerve length ratio are applicable to this character also.

In this study the successive position of the leaves on the shoot has strictly been observed. The angles are called "a, b, c" as is indicated in Fig. 1.

The precise measuring of these angles was often very difficult, especially in full-grown leaves where the nerves are generally rather strongly curved. For this reason the angles have always been measured at the origin of the nerves and not they were derived from the arc at the circumference of the leaf.

Though these angles could rarely be measured with a measuring error of less than 2 or 3 degrees, it is, because of the rather great number of leaves that we have measured, to be expected that the plus and minus deviations will have counterbalanced each other.

TABLE X

Average value of the angle between the nerves in leaves belonging to the classes A and C in *Acer cappadocicum.*

Positions of the leaves	Number of leaves	Nerve 1 in mm.	Angle a in degrees	Angle a VC	Angle b in degrees	Angle b VC
A	50	38	45,4	1,4	44,6	2,2
	50	50	43,6		42,6	
	50	65	39,4		39,5	
	50	84	37,0	0,95	36,5	1,6
C	50	32	51,4	1,4	53,6	2,4
	50	46	48,4		49,5	
	50	63	46,2	1,2	45,9	2,1

a) *The size of the angle between the nerves in the leaves of Acer cappadocicum*

As in the leaves of *Acer palmatum* var. *septemlobum* the angles between the nerves are rather small, those of *Acer cappadocicum* with their 2 large angles between the nerves were chosen for this study.

The result of the measurements of groups of 50 leaves belonging to the classes A and C is given in Table X. In the first place it is clear that both these angles in leaf class A as well as in leaf class C decrease as the leaf increases in size and that leaf class C always shows a larger angle than leaf class A. The V C is always lower in the larger leaves than in the smaller ones. The decrease of the V C is here too to be taken as expressing an approach to the ideal value. In order to determine the ideal value of these angles with greater precision, they were studied also in shoots with resp. 2, 3 or 4 leaf pairs (Table XI).

TABLE XI

Average values of the angle between the nerves and their V C in leaf class A on shoots of *Acer cappadocicum* with 2, 3 and 4 leaf pairs.

Number of leaf pairs in the shoots	Number of leaves	Nerve 1 in mm	Angle a		Angle b	
			in degrees	V C	in degrees	V C
2	100	67	39,9	0,88	39,2	0,84
3	100	80	37,7	0,58	34,0	0,65
4	100	83	35,7	0,58	33,4	0,82

From the figures of this table it appears that the angle between the nerves shows the lower V C in leaf class A on shoots with 3 leaf pairs, i.e. at exactly the same place where the lowest V C for the average nerve length ratio was found (Table VI).

For this reason we determine the ideal value of the angles in this species for angle a at 38 degrees and for angle b at 34 degrees.

b) *The size of the angle between the nerves in the leaves of Platanus acerifolia*

In the same manner as in the foregoing species the average value of the angles a and b were measured in this tree (Table XII).

It appears from this table that these angles decrease but little during the ontogenetic development of the leaf, whereas the V C shows a well-marked decrease.

In the same manner as in our study of the nerve length ratio the angles in leaves belonging to the classes E and G were measured in shoots with a different number of leaves in order to determinate the ideal value of these angles with more precision (Table XIII).

Here it appears that with an increase in the number of leaves per shoot also an increase occurs in the average size of the angles between the nerves, whereas the V C at the same time shows a decrease. The values with the lowest V C can be taken as representing the ideal size of the angle in this species. Thus the ideal value for angle a proves to

TABLE XII

Average size of the angle between the nerves and their V C in the leaf classes A, E, and G in *Platanus acerifolia*.

Position of the leaves	Number of leaves	Nerve 1 in mm	Angle a in degrees	Angle a V C	Angle b in degrees	Angle b V C
A	100	24	40	1,45		
	100	42	39	1,49		
	100	76	40	1,33	33	2,9
	100	105	39	1,16	35	2,8
E	100	170	45	0,66		
G	100	135	48	0,68	40	0,75
	100	175	47	0,65	39	0,69

TABLE XIII

Average size of the angle between the nerves in leaves of the classes E, G, I in shoots with a different number of leaves in *Platanus acerifolia*.

Position of the leaves	Class to which the top leaf of the shoot belongs	Number of leaves	Nerve in mm	Angle a		Angle b	
				in degrees	V C	in degrees	V C
E	E	100	160	45	0,66	39	0,92
	> G	100	175	46	0,59	40	0,85
G	G	100	160	46,4	0,55	36,0	0,76
	> I	100	181	46,4	0,61	38,6	0,55
		100	171	48,2	0,62	40,2	0,49
I	I	100	146	52,2	0,61	41,9	0,50

be 47,3 degrees and that for angle b 39, 4 degrees, and these values are found in leaves belonging to class G in shoots in which the top leaf belongs to leaf class I (or to a higher class).

Finally it appears that in the leaves of *Acer* the largest angle is accompanied by the highest V C, whereas in the leaves of *Platanus* the largest angle shows the lowest V C. The absolute size of the angle, therefore, can not be taken as indicating the degree of the development. However, when we see that, as a leave increases in size and thus attains a higher degree of development, the V C of its angle decreases, than the conclusion is admissible that here too the lowest V C is a criterium for the highest degree of development of the character, i.e. for what we have called its ideal value.

It seems justified, therefore, to determine the ideal value of the angle between the nerves in the leaves of *Platanus* as we have done above, i.e. on account of its lowest V C.

II. C THE NERVE LENGTH RATIO AND THE SIZE OF THE ANGLE BETWEEN THE NERVES IN LEAVES OF *Tropaeolum lobbianum Veitch*

In all the preceding investigations we have regarded the equality or inequality of the average nerve length ratio and of the size of the angle between the nerves in small and large leaves as indicating the absence or presence of changes in these characters during the process of growth.

By comparing average values a conclusion, therefore, was drawn with regard to a change in the form of the leaf, although we did not actually study the latter's ontogenetic development.

It is clearly desirable that leaves should be measured in successive growth stages in order to obtain a direct answer to this question.

This we have done in leaves of *Tropaeolum lobbianum* by means of contact photos, which were taken during the whole course of development. The latter beginning with a just measurable stage and ending with the final stage.

This leaf is very suitable for such a study, because it is from a very young stage totally flat, it is moreover totally glabrous and it has a very smooth outline and easily distinguishable main nerves.

In order to collect material for comparison first the average nerve length ratio and the average size of the angle between the nerves with their V C were calculated in groups of 50 leaves taken from successive position on the shoots: these leaves are indicated from now on as "detached-leaves".

Because in the parallel study the number of leaves was limited necessarily, of these detached-leaves too only groups of 25 were measured: by combining these groups of 25 in pairs, groups of 50 were formed: these groups are indicated as "leaf class BC, DE, FG etc".

The leaf class A is omitted because of its irregular shape and also because its nerves are, in a morphological sense, not yet fully developed.

Since only the nerves 1, 2 and 3 extend unto the margin, the study of the nerves and their angles had been limited to these ones (Table XIV).

TABLE XIV

Nerve length ratio and size of the angle between the nerves in "detached leaves" of *Tropaeolum lobbianum*.

Position of the leaves	Number of leaves	Nerve 1 in mm	nerve length ratio		Angle		Variation coefficient			
			Nerve 2	Nerve 3	a	b	nerve 2	nerve 3	angle a	angle b
BC	50	10	98	72	56	50	1,9	2,9	1,6	1,7
	50	39	101	85	52	47	0,95	1,4	2,1	1,6
DE	50	39	97	87	49	49	0,55	1,1	1,0	1,1
FG	50	10	94	77	51	49	0,95	1,8	1,3	1,8
	50	44	98	88	47	47	0,51	1,4	1,4	1,0
HI-etc	50	86	98	89	42	44	0,34	0,92	1,1	1,2

On the whole we observed here the same phenomena as in our preceding studies, viz. an increase of the nerve length ratio as the leaves become larger, and also according to the successive position of the leaves on the shoots till the highest value is reached in the leaf class HI, which also shows the lowest V C: the size of the angles between the nerves too decreases during the growth of the leaf and also from the lower to the higher leaves; the irregularity in the decrease of the V C will be discussed hereafter. We will take the leaf belonging to the class HI as the most ideal one, although a more precise determination of the ideal value has been omitted as it seemed superfluous in this case.

Apart from the study of these "detached-leaves" some other leaves were photographed in their successive stages of development. In this manner 50 series were formed of leaves belonging to class BC and class FG, which furtheron will be called "series-leaves".

In studying the nerve length ratio and the size of the angle between the nerves in each of these series of photos separately, we found that some of them increase, whereas others remain unchanged or show a decrease.

The different nerves and angles of the same leaf show a large degree of independence in their nerve length ratio and in the size of the angle between the nerves.

When we calculate the average values of these "series-leaves" in the same manner as we have done for the "detached-leaves", the same rules emerge (Table XV).

TABLE XV

Nerve length ratio and size of the angle between the nerves and their V C in the "series-leaves" of *Tropaeolum lobbianum.*

Position of the leaves	Number of leaves	Nerve 1 in mm	nerve length ratio		Angles		Variation coefficient			
							nerve length ratio		angle	
			nerve 2	nerve 3	a	b	2	3	a	b
BC	50	11	94	79	54	48	0,88	1,3	1,2	1,6
	50	28	98	86	48	48	0,81	1,1	1,6	1,3
FG	50	11	94	79	51	48	0,54	0,77	0,9	1,0
	50	30	97	85	47	46	0,48	0,71	1,0	1,0

However there is a difference in the absolute values of the nerve length ratio in so far as they are lower in the "series-leaves" than in the "detached-leaves". The difference is too large to be neglected: a plausible explanation can be found, however, in the circumstance that the series-plants developed under unfavourable conditions. They were cultivated in pots, whereas the "detached-leaves" were taken from plants that were growing on a bed in the garden. Moreover the potplants were cultivated in the early summer in a period of abnormally little sunshine and of low temperature (summer 1954).

These plants remained small and the largest leaves occurred in the leaf class EF, whereas but a few leaves were developed afterwards. The plants on the beds in the garden have, on the contrary, reached a very full growth: their shoots have produced sometimes a great number of leaves (up to leaf M). Meanwhile remembering the word of Mendel (1865) "No one will seriously maintain that in the open country the development of plants is ruled by other laws than in the garden bed" (otherwise in the pot: J. M.), we will seek the explanation of the difference between the pot- and full-ground-plants in a relation of some other kind.

In our attempts to determine ideal values in the leaves of *Acer* and *Platanus* with greater precision, we noted that the nerve length ratio as well as the size of the angle between the nerves differred considerably in shoots with a different number of leaves: the leaves of shoots with one leaf pair showed a lower average value than those with 2 or 3 leaf pairs. A similar difference will presumably have paid a part in this case.

We should compare the "series-leaves" with the less developed leaves of the shoots with 1 leaf pair, whereas the "detached leaves" would be comparable to those of the better developed shoots, i.e. those with a large number of leaf pairs.

On account of the results to which our studies so far have led, we feel us justified in drawing conclusions from the comparison of average values calculated in groups of corresponding parts with regard to the degree of development of definite specific characters.

TABLE XVI

Number of leaves which show the various differences in nerve length ratio and in the size of the angle between the nerves, observed between the initial and the final stage in the series of photos from the leaves BC and FG in *Tropaeolum lobbianum.*

Difference in per cents between initial and final stage	Nerve 2				Nerve 3			
	Leaf class BC		Leaf class FG		Leaf class BC		Leaf class FG	
0	2		5		0		3	
	—	+	—	+	—	+	—	+
1, 2, 3.	6	13	5	9	2	3	3	12
4, 5, 6.		14	1	23	1	6		7
7, 8, 9.		8		3		15		12
10, 11, 12.		5		2		12		6
13, 14, 15.		2				6		3
16, 17, 18.						3		2
19, 20, 21.						1		—
22, 23, 24.						1		1

Difference in degrees between initial and final stage	Angle a				Angle b			
	Leaf class BC		Leaf class FG		Leaf class BC		Leaf class FG	
0	1		1		12		13	
	—	+	—	+	—	+	—	+
1, 2, 3.	10	1	21	1	16	10	22	5
4, 5, 6.	21		25		6	5	8	
7, 8, 9.	13		2			1	1	
10	4						1	

However, we should never forget that but few specimens conform precisely to the average. We have studied by means of our photos how the nerve length ratio and the size of the angles between the nerves increase or decrease in each of 50 leaves belonging to the classes BC and FG. To this end we calculated the difference in the nerve length ratio and the size of the angle between the nerves that appeared between the first and last stage (Table XVI). This table shows that the nerve length ratio for nerve 2 shows much less extreme differences than that from nerve 3, and that leaves with small differences are more numerous than those with larger ones.

A similar difference is found between the leaves of class FG and those of class BC: this is in good agreement with the fact that the lowest V C is found in the largest leaves of class FG.

The angle a shows only in 2 % of the cases an increase, and the latter, moreover, is very small, whereas the angle b shows in 21 % of the leaves an increase, and this increase is sometimes very large. This explains why for the angle b the difference between the average calculated for the first and last stage is so small: the increase and the decrease of this angle counterbalance each other.

For the angle a, with its stronger decrease in the leaves of class BC as well as in the leaves of class FG, it is much easier to see that it behaves in conformity with the rule that the size of the angle decreases during the growth of the leaf. The large number of leaves that show little or no change in size of the angle b explains perhaps the lack of regularity in the V C that appears in Table XV.

The fact that in the leave belonging to class FG extreme differences between the first and the last stages are much less numerous and also smaller, demonstrates a decrease in the variability that manifests itself in the value of the V C.

II. D. THE LENGTH OF THE LEAF BLADE

In the course of our study of the nerve length ratio and of the angles between the nerves we could not fail to note that the length of the leaves too varies according to a definite rule.

In order to investigate this rule we have measured during the later part of the summer, i.e. at a time when the growth of the leaves, with few exceptions, is completed, in some plant species the length of the blade in leaves occupying different positions on the shoots. To this end the length of nerve 1 was measured.

a) *Acer palmatum var. septemlobum*

In Table I the average length of nerve 1 in leaves occupying successive positions on the shoots has been given; it appears that here too the highest average value is found in leaves of class A, and that the highest leaves show a decrease in the value of the average: the values for the length of the leaves form a similar kathodic series as we found for the nerve length ratio and for the size of the angle between the nerves.

A more precise determination of the ideal length is to be found in Table IV, where the V C's are given. As the lowest value for the latter is to be found at a length of 49 mm, which occurs in leaves of class A on shoots with 3 leaf pairs; it is this value that is to be regarded as the ideal one.

b) *Acer cappadocicum*

From Table V it appears that the leaves of class A show a higher average length than the leaves of class C: this series too is a kathodic one. A more precise determination of the ideal length is to be found in Table VI. Exactly as we found for the nerve length ratio and for the size of the angle between the nerves, the average length of leaves belonging to class A in shoots with 3 leaf pairs shows the smallest V C, so that here the ideal length is to be located.

c) *Platanus acerifolia*

In 4 trees (P, Q, R, S), which were all of about the same height (± 10 m), the average length of the leaves was determined. Moreover in Q the influence of the position the leaves occupy on the tree, was studied. To this end groups of 150 leaves occupying different positions on the shoots and taken partly from the lower branches and partly from branches near the top, i.e. at a height of 8–10 m, were measured (Table XVII).

TABLE XVII

Average length of leaves in different trees of *Platanus acerifolia*.

Tree	Position of the leaves on the shoot	Number of leaves	Position of the shoots on the tree	Aver. length in mm	V C
P	A	150	at the bottom	73	2,3
		150	at the bottom	68	2,3
		150	at the bottom	77	2,1
	D	150	at the bottom	155	0,8
	E	150	at the bottom	168	0,7
	G	150	at the bottom	180	0.6
Q	A	150	at the bottom	63	1,8
		150	at the top	66	2,1
		150	at the top	67	1,8
	D	150	at the top	137	0,7
		150	at the bottom	138	0,6
	F	150	at the bottom	143	0,8
	G	150	at the top	143	0,9
R	G	150	at the bottom	180	0,8
S	A	150	at the bottom	73	2,0

This table shows that:

1) the average length shows an increase in the direction of the

higher leaves with the highest value in the leaves of class G; the value found for the length form like those for the nerve length ratio and for the size of the angle between the nerves an anodic series:

2) that the leaves of the lower branches and those from the top region do not show any difference in this respect:

3) that the highest average is accompanied by the lowest V C.

A more precise determination of the ideal value is to be found in Table VIII (and XIII), for which the material was collected from other trees than P, Q, R, S.: this ideal value amounts to 175 (176) mm and is found as well in the leaves of class E as in those of class G, at least in the shoots with the larger number of leaves. It is noteworthy that the V C of the 2 groups of 100 leaves shows hardly any difference, which apparently means that these figures are trustworthy.

It is in the meanwhile very strange that the average values found for all leaf classes in tree "Q" are so much lower than those found in the other trees that the difference can not be neglected as unimportant. This phenomenon is the more remarkable as our study of the nerve length ratio did not reveal such a difference.

We may perhaps find an explanation of this different behaviour in the age of the tree: this one was older than the others- or else in the circumstance that *Platanus acerifolia* is a hybrid.

From the study of these 3 kinds of leaves (*Acer palmatum* var. *septemlobum*, *Acer cappadocicum* and *Platanus acerifolia*) it appears that the variability of the length is determined for the greater part by the position of the leaf on the shoot, and that the greatest length is accompanied by the lowest V C.

II. E. Relation between the length of petiole and lamina

In *Acer platanoides* and *Acer pseudoplatanus* and in *Batrachium fluitans* the average length of the petiole was measured and this value was expressed in per cents of the length of the lamina: its V C was determined too. The leaves were arranged in groups according to the position they occupied on the shoot (Table XVIII). The two species of *Acer* show a rather similar result. In the full-grown leaves of class A the average length of the petiole amounts to 170 mm and they are about 3½ times longer than in the higher leaves belonging to the classes C D. In the lower leaves the petiole is longer than the blade, whereas it attains in the higher leaves hardly 60 % of the blade length.

The values found for the average length of the petiole form, like those found for the blades, a kathodic series with the highest value in the leaves of class A, and here too we find the lowest V C. The greatest length is, therefore, accompanied by the lowest variability.

In *Batrachium fluitans* the leaves were grouped in the same way as in our study of the nerve length ratio (see Table IX). From the data of Table XVIII it appears that the petioles of this species are absolutely (their length in mm) as well as relatively (the length of the petiole expressed in per cents of the length of nerve 1) best developed in group I (leaves ABC), and here too we find once more the lowest V C.

It is very remarkable that the variability of the nerve length ratio reaches its lowest value in the groups IV and V, whereas the petioles show in these groups the highest variability. We observe also in the values found for the average length of the leaf blade in leaves occupying successive positions on the shoot an anodic series, and on the contrary a kathodic series in the values for the length of the petiole.

Finally it appears here again that the highest degree of development of the petiole is accompanied by the lowest degree of variability.

TABLE XVIII

Average length of the petiole expressed in per cents of the length of nerve 1 in *Acer platanoides*, *Acer pseudoplatanus* and *Batrachium fluitans*.

Species	Position of the leaves	Number of leaves	Length nerve 1 in mm	Length of the petiole in mm	Length of the petiole in per cents of the length of nerve 1	V C
a) Acer platanoides	A	40	55	59	108	1,11
		40	125	175	140	0,80
	D	40	85	51	63	3,1
b) Acer pseudoplatanus	A	40	55	47	86	3,6
		40	95	105	111	3,3
		40	140	171	122	2,0
	C	40	45	24	54	4,4
		40	80	47	59	4,1
c) Batrachium fluitans	ABC	50	72	73	102	
		50	154	154	100	2,5
	DEF	50	73	49	68	
		50	183	137	75	2,7
	GHI	50	100	55	55	
		50	202	125	62	3,0
	JKL	50	104	33	32	
		50	198	73	37	7,6
	M/V	50	60	8	13	
		50	174	36	21	10,4

II. F. Relative leaf width

Heuser (1915) has already observed in wheat that there is a correlation between the width of a leaf and its position on the shoot; in this species the leaves increase in width as they approach the top of the shoot.

Abbé, Randolph and Einset (1941) too have observed that the width of the leaf in a variety of corn increases with about 9 % in each successive leaf. In their study they included the leaf primordia and they observed that here too occurs an increase in size that goes parallel with the increase in width in the full-grown leaves.

Snow and Snow (1937) have observed that on the surface of the apex a definite minimum space is required for the development of a new leaf. It is possible (and almost to be expected) that there too a variability is present which determines the rate of growth of the leaves that are formed.

The studies which have been instituted in this direction indicate that, as Pearsell and Hanby (1926) express it: "It is clear that the main factor determining the shape of the leaf is the rate of growth in the leaf initial" (primordium, J. M.) (p. 120). The question as to the cause of the variability is transferred by these observations from the full-grown leaves to the apical meristem. This does not simplify the solution of this problem, because there is (at least apparently) a striking similarity between the apices in most plant species.

In a great number of leaves collected from different bushes of *Ligustrum ovalifolium* L, and from different successive positions on the shoots of the latter, the length and the width have been measured: then the width was expressed in per cents of length.

In the measurements the following difficulties occurred. The top of the leaves belonging to class A is often found in a withered state; the rounded form of the top of many leaves suggests that here the withered part has already fallen off: such leaves may have a width of 80 % and more.

Moreover, the leaves belonging to the classes A and B, which have a length of a few millimeters only, are very difficult to measure: and it is often impossible to see where the leaf really begins; petiole and blade are often gradually merging one into the other. Notwithstanding these difficulties the values found for the average width in groups of 10 leaves already yield a rather trustworthy result, for they show a handsome similarity; it is not so much the absolute value of the figures but rather the decrease or increase of the successive values for the average which here, as in all similar instances, are of importance.

TABLE XIX

Leaf width in per cents in *Ligustrum ovalifolium*.

Position of the leaves	Number of leaves	Nerve 1 in mm	Leaf width in %	Position of the leaves	Number of leaves	Nerve 1 in mm	Leaf width in %
A	10	2	78	G	10	10	41
	10	4	81		10	15	47
	10	8	75		10	27	49
	10	12	76		10	50	48
	10	16	63		10	65	48
	10	18	69		10	75	48
					10	78	46
B	10	7	70		10	83	48
	10	9	73		10	93	48
	10	12	69				
	10	13	64	P/Z	10	61	48
	10	18	68		10	69	46
	10	24	66		10	79	47
	10	26	62		10	85	48
	10	29	63				

From Table XIX it appears that the leaves of class A show the greatest relative width, and that the latter decreases from 80 % to 70 % when we proceed from the smallest to the largest leaves. The width of leaves belonging to class B decreases from 70 % to 63 %; those of class G and the higher leaves show for each length an average width of ± 48 %.

This decrease in width can be attributed to a rather strong difference in the rate of growth between the upper and lower half of the leaf. In the leaves of the classes A and B the top half develops at first very strongly so that the top often will already be withered when the basal half is still growing; in this leaf the growth is, according to the terminology of Prantl (1883), apparently basiplastic. In the leaves that occupy a higher position on the shoot, growth becomes more equally spread over the whole surface, and then the relative width remains unchanged.

In order to diminish the effect of accidentally present extremes on the V C, the groups of 10 leaves have been combined into groups of 20 leaves (Table XX).

TABLE XX

Variation coefficient of the leaf width in *Ligustrum ovalifolium.*

Position of the leaves	Number of leaves	Nerve 1 in mm	Width of the leaves in %	V C
A	20	3	80	4,2
	20	10	76	3,5
	20	17	66	2,8
B	20	8	72	2,2
	20	12	67	3,5
	20	21	67	2,4
	20	27	63	2,6
G	20	13	44	3,0
	20	39	49	2,6
	20	70	48	2,0
	20	88	48	1,7
P/Z	20	65	47	2,0
	20	82	48	1,8

When the small deviations found in the leaves belonging to class B, which can be attributed to the relatively small number of leaves and to measuring difficulties, are left out of consideration, we may conclude from these data that in each leaf class the V C decreases when the size of the leaves increases, and also when we proceed from the lower to higher leaves until the highest value is reached in the leaves belonging to class G.

Here again it appears that the rate of the variability decreases as the character, here the relative width, reaches a higher degree of development.

One might perhaps object against my accepting the relative width of 48 % as the ideal value because the leaves of class A show a relative width of 80 % and more. However, if we take the absolute width in mm, than the leaves of class G show the highest value. Moreover we may add that in a leaf with a width of 80 % the development was checked by the withering of the top part. For this reason this width is not to be accepted as a normal one, and it can, therefore, not express the ideal form of the character.

II. G. Number of umbel rays

In all the foregoing studies there was always a greater or smaller possibility that measuring errors might partly obscure the real situation, although they were never of such importance that the results could have been influenced to a marked degree. Yet it might be useful to supplement these studies into class-variability with one of discrete variability, where measuring errors, if not wholly excluded, are limited to a minimum.

We believe to have found an ideal object for a study of this kind in the umbel rays of *Aegopodium podagraria L.* In the thousands of umbels of which the rays were counted by us, it has happened but seldom that there arose any doubt with regard to the number of these rays.

As the foregoing studies have shown that a definite arrangement of the part according to the position they occupy in the plant is of primary importance in the study of variability, it was our first task to discover in this plant species a suitable arrangement of the umbels of which the rays were to be counted.

In the at first sight rather disorderly arrangement of the umbels of this species a distinct order is to be detected if one pays attention to the manner of branching in this species and to the succession in which the umbels expand.

Thus at the top of the main stem we always find a single umbel, and this proves to be the one that flowers first. It is born by a peduncle at the basis of which we find at least one leaf; this umbel is indicated with the letter "A" (Fig. 4). At the basis of this peduncle arise a number of other peduncles (sometimes 5) which in their turn end in an umbel. These umbels are flowering somewhat later than umbel A, and they are indicated as "B". Lower on the stem there sometimes arise once more one, two or three peduncles ending in umbels that flower after the umbel "B", and that are named "C".

Below these inflorescences some peduncles, each again with an umbel at the top, may arise, but these peduncles always arise single from the main stem: they are called "D, E, F, G"; the umbel G was only found twice among 500 plants.

On the peduncle of umbel A as well as on the other ones occasionally a small branch with a single umbel at the top (secundary umbel) may arise: the rays of these umbels were not counted. The 500 plants were collected from the most different surroundings: in all 49443 umbel rays were counted.

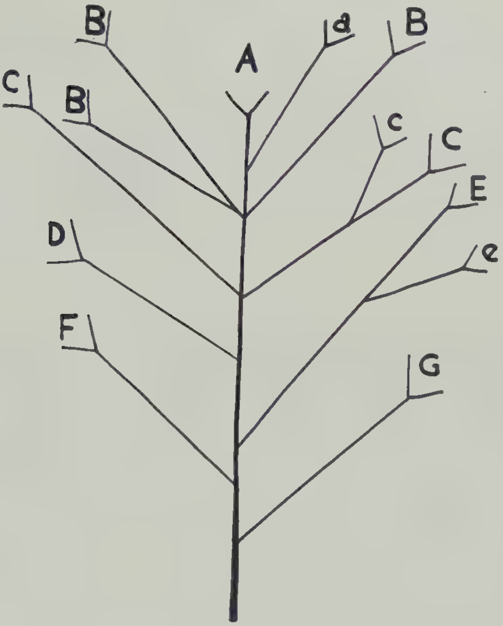

Fig. 4. Sketch of the position of the umbels in *Aegopodium podagraria.*

These 500 plants were divided in 5 groups according to the number of umbels of the classes A, B, C etc. that were present, viz.

Group I with 6 kinds of umbels belonging to the classes A–F
,, II ,, 5 ,, ,, ,, ,, ,, ,, ,, A–E
,, III ,, 4 ,, ,, ,, ,, ,, ,, ,, A–D
,, IV ,, 3 ,, ,, ,, ,, ,, ,, ,, A–C
,, V ,, 2 ,, ,, ,, ,, ,, ,, ,, A–B

Since the number of umbels belonging to each of the classes was different (each plant has only 1 umbel of class A but on the average 2 umbels of class B), the V C of the average number of umbel rays was for each class adjusted to a basic number of 100 umbels (Table XXI).

When we look at the average number of rays that are found in the different umbel classes we notice in each group an anodic series, which has nearly always its summit in the umbels belonging to the last but one class.

The increase in the average number is accompanied by a decrease of the V C.

The group of umbels with the highest number of rays (an average of 21,3) is that found in class D of group I with a V C of 1,24 (I D), whereas the group of umbels belonging to class C of group II (II C) shows an average of 20,2 rays with a V C of 1,20.

We are now confronted with the question whether the ideal number of rays is to be seen in class I D or in II C. If we compare the groups I and II, it will be clear that for all corresponding umbel classes the V C is in group II lower than in group I.

We need not attach any value to the exception formed by umbel class A, which shows in group I a lower V C than in group II, as the high value of the V C indicates a high degree of instability, so that occasionally too high or too low value may be expected. Because of the fact that the V C decreases in each group the nearer we come to the umbel class with the highest number of rays and according to the rule that we found repeatedly confirmed in the preceding studies, viz. that the ideal value is recognizable by the lowest V C, the ideal value of the number of rays is for this species represented in the umbel class IIc in plants with 5 umbel classes (A, B, C, D, E): and it amounts to 20,2 umbel rays.

TABLE XXI

Aver. numbers of rays per umbel and its V C in *Aegopodium podagraria.*

	Group I			Group II			Group III			Group VI			Group V		
Position of the umbels	Number of umbels	Aver. number of umbel rays	V C	Number of umbels	Aver. number of umbel rays	V C	Number of umbels	Aver. number of umbel rays	V C	Number of umbels	Aver. number of umbel rays	V C	Number of umbels	Aver. number of umbel rays	V C
A	70	13,4	1,9	180	13,7	2,2	130	14,9	1,9	100	16,2	1,51	20	16,0	0,93
B	120	18,6	1,44	375	18,2	1,4	269	18,4	1,44	205	19,4	1,29	37	17,0	1,4
C	88	20,0	1,35	215	20,2	1,20	135	19,8	1,36	100	19,3	1,50			
D	70	21,3	1,24	180	20,4	1,22	130	18,6	1,6						
E	70	21,2	1,38	180	19,7	1,35									
F	70	20,2	2,7												

Among the 2263 umbels of which the number of rays was counted, we did not find a single one with 6 or 30 rays, but we found one with 5 and one with 31 rays resp. in class A of group III and B of group IV. These extreme variates were not found in plants with the smallest but with the greatest variability.

Here we notice once again that a high degree of variability does not indicate a high grade of development, but on the contrary, a low one.

Everybody will recognize in an umbel with but 5 rays a kind of "failure". But the umbel with 31 rays is just as well an excess as the other. In this light it is not to be wondered that the ideal value of a character is often not found in parts with the highest value; the lowest V C ,however, is always a reliable indication.

III. TESTING OF THE RULES OBSERVED ON DATA DERIVED FROM OTHER INVESTIGATORS

In the literature many studies into the variability of characters are to be found. In some of them the data are given in so much detail that it is possible to apply our own method of investigation to them. In order to extend the scope of the divergent characters our choice has fallen on A) the size of the leave meshes: B) The relative length of internodia and C) the ratio of the number of stomata and the number of epidermis cells.

A) THE SIZE OF THE LEAF MESHES

BENEDICT (1915) has calculated in *Vitis vulpina L* the size of the meshes between the ultimate ramifications of the nerves in the leaves of young and old plants. He concludes that these meshes are greater in young plants than in older ones. His figures and photos very clearly show a gradual decrease of the size of these meshes with the increase in age of the plants.

He has given a very detailed account not only of the size of these meshes from plant to plant with a record of the age of the latter, but also according to the position the leaves occupy on the shoot. In order to obtain a more easy comparability with our own data we have indicated the successive positions occupied by the leaves on the shoot from the base to the top with the letters A, B, etc. and not with a figure as Benedict has done.

When we calculated from the data given by Benedict the average size of the meshes and its V C for the leaves belonging to the classes A–J in young and old plants we arrived at the results given in Table XXII. From this table it appears that the largest meshes are found in the youngest plants and that the V C likewise is here lower.

TABLE XXII

Aver. size of leaf meshes in respect to the age of the plants in *Vitis vulpina.*

Age of the plants in years	Position of the leaves	Number of leaves	Aver. size of the leaf meshes in square mm	V C
3–5	A–J	42	0,498	0,94
35–70	A–J	45	0,169	2,6

Next to this the average size of the meshes and its V C was determined for leaves of the classes AB and IJ from the 10 youngest and the 10 oldest plants (Table XXIII). It is clear that the meshes are smaller in the higher leaves and the more so as they are taken from older plants. Here too the lowest V C is found in the leaves of the class AB of the youngest plants, i.e. in the leaves which show the largest meshes. Our final conclusion is that the width of variability decreases when the size of the meshes increases or when the leaves reach a higher degree of development.

TABLE XXIII

Aver. surface of leaf meshes in respect to the position of the leaves on the shoots at *Vitis vulpina*.

Age of the plants in years	Position of the leaves	Number of leaves	Aver. surface of the leaf meshes in square mm	V C
3–10	A. B.	20	0,440	3,2
	I. J.	20	0,434	3,7
25–70	A. B.	20	0,205	3,7
	I. J.	20	0,186	4,3

We may regard the decrease in the size of the meshes as the plants grow older as a decline, a sign of senility. In the opinion of *Benedict* photosynthesis and the capacity for water absorbtion decrease as the plant grows older: at the same time the number of stomata increases but their width decreases: the palissade tissue too is less developed.

It is, therefore, in every respect reasonable to see in the decrease in the size of the meshes a decline.

B) The relative length of the internodia

T. Tammes (1903) has studied the question whether in shoots of *Fagus sylvatica* the length of the internodia undergoes a change when the leaves are removed. She concluded that the absolute length of the

TABLE XXIV

Length in per cents S D and V C of the internodia in shoots of *Fagus sylvatica* (T. Tammes. 1903. p. 79)

Position of the internodia on the shoots	B	C	D	E	F	G	H	I	Total length of the shoots in mm
	0,5	2	8	15	18	20	22	14	258
	0,5	4	13	15	17	19	19	12	244
	1,0	6	10	13	17	21	19	11	344
	0,5	2	9	14	18	20	22	14	224
	1,0	5	11	14	18	19	19	14	283
	0,5	3	10	16	18	20	19	13	253
	0,5	3	10	14	16	20	22	14	269
	1,0	5	12	13	17	19	19	14	301
	1,0	1	10	16	18	20	20	12	253
	0,5	0,5	8	16	18	19	21	16	248
	0,5	1	2	13	21	23	23	17	196
	0,5	1	5	17	20	21	21	14	182
	1,0	5	7	13	16	20	23	19	279
	0,5	3	9	11	15	19	22	18	326
	0,5	3	10	13	16	19	20	18	341
Aver. %	0,76	2,96	8,93	14,2	17,8	20,6	21,1	15,0	Aver, length 263
S D			0,72	0,42	0,42	0,29	0,40	0,63	
V C			8	3	2,45	1,45	1,90	4,2	

internodia becomes smaller but that the relative length remains unchanged. She rightly decides that the relative length of these internodia may be regarded as characteristic for this species.

From her data we have chosen one series, and to this series we have applied our method: however, we have first expressed the length of the internodia in per cents of the total length of the shoot (table XXIV).

She has only measured the internodia of 15 shoots of *Fagus sylvatica* but this number will be sufficient to show that the variability in the length of the internodia decreases as the length increases. It is noteworthy that the lowest V C is not found in the longest internodia of class H but in those of class G, and for this reason we recognize these internodia as the ideal ones, but we admit that this idea has here but a dubious value.

The only important fact brought to light by this study is, that the development of this character, the relative length of the internodia, towards its ideal value is on the whole accompanied by a decrease of the variability.

C) THE RATIO BETWEEN THE NUMBER OF STOMATA AND THE NUMBER OF EPIDERMIS CELLS

BEDAUX [1] (1954) has studied the so-called stomatal index in the leaves of *Teucrium chamaedrys L.*

The stomatal index is the figure that indicates the ratio between the stomata number of and the number of epidermis cells. This relation is expressed in the formula: $I = \frac{100 \times S}{E + S}$; in which S indicates the number of stomata on the lower side of the leaf: (the two guard cells of one stoma are taken as one), and E indicates the number of the epidermis cells on the lower side of the leaf.

In his study BEDAUX always paid attention to the position of the leaves on the stem, because other investigators had found that there was an acropetal increase in the frequency of the stomata. By way of controll he has studied the index in 10 successive leaf pairs of one plant.

From his data we have calculated the average value of I, its S D and V C for all leaf pairs as they occur at the plant from the base to the top of the stem: because the number of measurements varied for the groups of leaf pairs from 16 to 24 the V C has been adjusted to a base of 20 for each group of leaf pairs (Table XXV).

Considering that the number of leaves per group was but small, the calculation of the V C yielded quite satisfactory results.

The decrease of the V C is strikingly regular and its V C is the smallest for leaf pair 9: with some reserve, because of the rather low number of measurements, the ideal value of the I is determined at 21,4 (It is remarkable that the value of I of all leaves together is 21,5).

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[1] I wish to express my indebtness to him for his kindness in allowing me the use of his data.

TABLE XXV

Average stomatal index S D and V C in leaves of *Teucrium chamaedrys* (Bedaux)

Position of the leaf pairs	Number of measurements	Aver. Index	S D	V C
1	22	19,5	0,79	4,1
2	24	20,4	0,84	4,1
3	16	22,8	0,87	3,9
5	20	21,1	0,80	3,8
6	20	21,8	0,75	3,4
7	20	22,6	0,69	3,1
8	20	22,7	0,74	3,2
9	20	21,4	0,63	2,9
10	16	21,0	0,63	3,0

On account of the rather small number of measurements it is not to be wondered that a regularity in the increase of the average in the successive leaf pairs is difficult to detect. As the lowest average is found in the leaf pair A the average values probably form here an anodic series. Finally we can see in these data once more a proof that a character varies less as it reaches a higher stage of development.

IV. SPREADING OF THE FREQUENCY OF THE VARIATES

Now that we have attained this point in our investigation, we will turn our attention to the question to what extent the numbers in which the different variates are met with, are identical with or different from those that is to be expected if one assumes that the spreading of the variates should be the same as in the mathematical probability curve or the binomium of Newton.

In order to study this question two divisions were formed from the data of our own studies: division I is made up of groups of data which showed a high V C: division II is made up of groups of data which showed the smallest possible V C.

Of course, the choice of the groups for the first division has been more or less at random: here our only aim was the collecting of groups with a strongly varying character, whereas the second division is made up of groups exhibiting characters which approached the ideal value: our final aim was to obtain as great a contrast as was possible.

Here we are only concerned with the number of variates that were found in each variation class, whereas it does not matter in the least that the groups of variates are of a totally different kind (nerve length ratio, size of angles between the nerves in different plant species).

From these different series of measurements we first have put the class with the mean value in one column beneath each other, and we have added up these figures in both divisions I and II.

After this the other classes of plus and minus variates are arranged in columns at equal distances from the mean class and the figures of each column too are added up (Table XXVI.) This table shows in the first place how many variates are found in each variation class: in this way the spreading of the 500 variates brought together in the divisions I and II over the various classes is obtained, moreover the number of variates in each class is expressed in per cents of the total number. Right at the bottom the percentages are given which were to be expected according to the mathematical probability calculus (the binomial figures). Under the table the nature of the various groups of which the two divisions have been formed, are specified.

From this table it appears that:

1) the frequency curve of division I shows for each group separately a top that is too low; and of course this applies to the curve in which they are all integrated, too.

2) in the groups with the ideal values (division II) the central classes show the nearest approach to the binomial figures: the class with the mean value shows this phenomenon most convincingly.

3) the classes of the most extreme plus and minus variates show relatively the greatest variability and the greatest deviations of the binomial values.

According to the mathematical probability calculus they should have had but a thousandth or a millionth per cent of chance, whereas they are really represented by 1 or 2 % of the total number.

The same method has been applied in *Aegopodium podagraria* to the spreading of the umbel rays over the different classes. Division I of Table XXVII is once more made up of strongly varying groups; division II of groups with low variability; the origin of these groups are indicated too.

We note here too in division II the nearest approach to the binomial values, whereas the mean class contains even a larger number of variates than would have been expected.

It appears, therefore, that the mean class as well as the classes of the extreme minus and plus variates are represented by a larger number of variates than should have been expected on account of the probability calculus. The mean class, therefore, becomes better represented as the ideal value is approached.

V. DISCUSSION AND CONCLUSIONS

Our investigations have led to the conclusion, that one of the various degrees of development that a character shows, should be regarded as the ideal one, and that this ideal development is recognizable by the decrease of the V C to its lowest value. This ideal development, or ideal value of a character, is, as we have seen, not necessary its highest value.

This view is supported by the following facts, all brought to light by our investigations;

1) Each character shows in its ontogenetic development (i.e. from its first appearence until it has reached the end of its development) a diminution in its variability:

TABLE XXVI

Class	—10	—9	—8	—7	—6	—5	—4	—3	—2	—1	Mea
Division I	—	—	2	3	2	3	5	7	7	7	17
	—	2	1	3	3	4	6	5	13	9	14
	—	—	1	2	4	5	7	9	9	18	16
	—	—	—	1	2	3	6	7	7	14	15
	2	6	2	8	6	8	6	8	11	2	8
	2	8	6	17	17	23	31	36	47	50	70
	0,4	1,6	1,2	3,4	3,4	4,6	6,2	7,2	9,4	10,0	14,
Division II	—	1	—	2	1	4	1	3	17	9	19
	—	—	1	1	—	5	6	9	9	14	12
	—	—	—	3	1	5	4	8	11	12	17
	—	—	—	—	—	—	4	9	11	13	20
	—	—	1	1	—	2	3	5	7	10	16
	—	1	2	7	2	16	18	34	55	58	84
	0	0,2	0,4	1,4	0,2	3,2	3,6	6,8	11,0	11,6	16,8
	0,000001	0,00002	0,0002	0,11	0,46	1,48	3,6	7,4	12,0	16,2	17,6

Division I

a) =	Platanus	Leaf I	Shoot I	nerve –2	(Table VIII)
b) =	Platanus	Leaf I	Shoot I	nerve –3	(Table VIII)
c) =	Acer palm.	Leaf A	Shoot 4–l.p.	nerve –2	(Table IV)
d) =	Acer palm.	Leaf A	Shoot 2–l.p.	nerve –2	(Table IV)
e) =	Acer capp.	Leaf A	Shoot 2–l.p.	nerve –3	(Table VI)

TABLE XXVII

Class	—10	—9	—8	—7	—6	—5	—4	—3	—2	—1	Mea
Division I	—	—	3	3	6	2	5	13	9	25	35
	1	—	—	3	3	5	4	9	10	23	20
	—	1	—	1	—	5	2	3	4	16	14
	—	—	—	—	—	3	5	7	7	9	8
	—	—	—	—	—	2	2	8	5	8	11
	—	1	—	2	3	4	13	16	22	27	23
	1	2	3	9	12	21	31	57	67	108	111
	0,14	0,28	0,41	1,2	1,6	2,9	4,3	7,8	9,3	14,5	15,
Division II	—	—	—	—	—	—	1	2	8	14	13
	—	—	—	—	—	—	2	6	12	8	11
	—	—	—	—	1	1	5	11	20	44	39
	—	—	—	—	3	—	3	13	16	28	40
	—	—	—	—	1	2	3	6	20	36	41
	0	0	0	0	5	3	14	38	76	130	144
	0	0	0	0	0,6	0,4	1,9	4,8	10,1	17,5	19,
	0,000001	0,00002	0,0002	0,11	0,46	1,48	3,6	7,4	12,0	16,2	17,

1	+2	+3	+4	+5	+6	+7	+8	+9	+10	Nr.	Division I
10	11	7	5	2	7	—	1	2	2	100	a)
7	8	5	6	5	5	2	—	—	1	100	b)
8	11	2	3	—	4	—	—	—	1	100	c)
11	8	6	6	10	—	2	—	2	—	100	d)
6	6	6	1	5	3	2	2	1	1	100	e)
42	44	26	21	22	19	6	3	5	5	500	
,4	8,8	5,2	4,2	4,4	3,8	1,2	0,6	1,0	1,0	per cents	
14	14	3	10	—	1	—	1	—	—	100	f)
15	12	5	5	2	3	—	1	—	—	100	g)
13	17	6	—	3	—	—	—	—	—	100	h)
19	10	6	6	2	—	—	—	—	—	100	i)
12	13	11	7	6	4	—	1	—	1	100	j)
73	66	31	28	13	8	—	3	—	1	500	
4,6	13,2	6,2	5,6	2,6	1,6	—	0,6	—	0,2	Per cents	
6,2	12,0	7,4	3,6	1,48	0,46	0,11	0,0002	0,00002	0,000001	Binom. relation	

Division II
f) = Acer palm. Leaf A Shoot 3–l.p. nerve –2 (Table IV)
g) = Platanus Leaf G Shoot > I nerve –2 (Table VIII)
h) = Acer capp. Leaf A Shoot 3–j.p. nerve –2 (Table VI)
i) = Acer capp. Leaf A Shoot 3–j.p. angle a (Table VI)
j) = Acer palm. Leaf A Shoot 3–j.p. angle a (Table IV)

+1	+2	+3	+4	+5	+6	+7	+8	+9	+10	Nr.	Umbel
20	18	12	8	8	—	2	—	1	—	180	II A
18	17	8	3	3	3	—	—	—	—	130	III A
23	16	7	5	2	1	—	—	—	—	100	IV A
8	6	2	5	2	4	2	2	—	—	70	I F
12	7	9	1	4	1	—	—	—	—	70	I A
24	14	11	6	4	6	2	1	—	—	180	
05	78	49	28	23	15	6	3	1	0	730	
4,4	10,7	6,7	3,9	3,3	2,1	0,8	0,4	0,14	0	Per cents	
13	9	9	8	5	3	2	—	1	—	88	I C
9	6	7	2	6	—	—	1	—	—	70	I D
33	11	18	12	5	1	4	—	—	—	205	II C
26	14	15	10	5	4	1	2	—	—	180	II D
28	27	18	10	8	2	2	—	1	—	205	IV E
09	67	67	42	29	10	9	3	2	0	748	
4,7	9,0	9,0	5,6	3,8	1,3	1,2	0,4	0,26	0	Per cents	
6,2	12,0	7,4	3,6	1,48	0,46	0,11	0,0002	0,00002	0.000001	Binom. relation	

2) In the series of average values obtained in the earlier described manner, i.e. by arranging the material in groups according to the position the parts occupy in the plants, an increase is always to be observed that is accompanied by a decrease of the variability width: it does not matter here, whether this series has its highest value at the base of the shoot (kathodic series) or at the top (anodic series).

The decrease of the variability width always points to a final state of development from which consistently is to be concluded that the lowest variation width is a criterium for the highest degree of development of a character, in the sense of its ideal value. The foregoing studies show that this ideal value is for each character and each species a constant one.

The view, that it is possible to detect for each character a constant value is not shared by all investigators. Klebs (1906) can be taken as the exponent of the opposite view. He says: "Dieses regelmäszige Schwanken um einen Mittelwert ist aber nicht aufzufassen als eine für irgend eine Pflanze notwendige Erscheinung, es ist nicht ein geheimes, inneres Gesetz, das als etwas in der Natur der Pflanze Gegebenes anzunehmen ist . . . . Die Wahrscheinlichkeitsrechnung ist eine Methode, die ganz unabhängig von der Natur des Gegenstandes ist und daher über diese Natur nichts auszusagen vermag.

Die Mittelwert eines Markmals, z.B. der Blattgrösze, der Internodienlänge, der Zahl der Blütenglieder usw. entspricht der am haüfigsten vorkommenden Kombination dieser Faktoren: die selteneren Varianten entsprechen den selteneren Kombinationen.

Aus dem gesagten folgt, dasz der Mittelwert keine konstante Grösze sein kann, sondern immer ein Resultat der gerade zufällig vorhandenen Bedingungen ist und sich mit diesen veränderen musz. Tatsächlich beobachtet man auch solche Veränderungen des Mittelwertes, wie Weisze, Macleod, de Vries nachgewiesen haben" (S. 304).

Klebs maintains therefore 1° that constant average values do not exist, and 2° that their non-existence is the necessary consequence of the inconstancy of the external circumstances. Indeed, with regard to statistical investigations carried out "independent of the nature of the object" the critical attitude of Klebs is justifiable. When we determine average values without paying attention to the predisposition of the parts, which depends upon the position they occupy, than these average values indeed vary according to accidental circumstances (see figure 2 and our exposition on p. 284 seq.).

Some people think that this is caused by the occasional presence of extreme variates. But in this manner the importance of the extreme variates is exaggerated. We should realize that in order to meet extreme variates, which, as everybody will admit, are relatively seldom, a very large number of the variates must be collected. But the larger the number of variates, the smaller is the influence of the extreme ones on the average.

Moreover there is no reasonable ground to assert that the extreme variates will be found in one direction only, either as minus or as plus variates. The chance to find minus variates is always the same as to find plus variates; as they counterbalance each other they will not, in general, influence the average.

When we collect parts without paying attention to the different positions they occupy, it are the different predispositions, which, as we have seen, are determined by the position of the parts, that influence the value of the average.

Under such circumstances it entirely depends on the position the collected parts accidentally occupied, what the average will be: the chance that in this case the ideal value will appear is practically nil, how great the number of the collected parts may be. However, by applying the above described method, i.e. by restricting the range of positions, from which parts are collected, more and more constant averages will be obtained. This is clearly shown by the outcome of our studies. It appears that the group of variates showing the more precise value of the average exhibits a lower degree of variability. Our investigations show, in direct opposition to the opinion of KLEBS, that it is really possible to find constant averages. The second assertion of KLEBS, which is merely an attempt to declare the first one, need not be considered, as the first is rejected by us.

This opinion with regard to the constancy of the ideal value of a character is not refuted by the fact that by changes of the circumstances the averages too may change. There is no reason to doubt the correctness of the data collected by WEISZE, MACLEOD, DE VRIES, KLEBS and many others, who have demonstrated that it is possible to obtain different averages by changing the environment. The reactions are obviously dependent in a large measure upon external agencies. But we will have to interpret this fact in this way that, when the circumstances are altered in a definite direction, the ideal state will not be attained any more, and the averages that under such circumstances are found, are none of them the ideal one.

We will now turn our attention to the question whether all these natural variations are to be ascribed to internal or to external agencies. Although we have always used the neutral term "variability" is was never our intention to deny the influence of external factors. But on the other side it seems to us that, on account of the data produced by our studies, one has to attribute a greater influence to internal factors than has generally been done.

Very often all variability is identified with modification, which means with changes that are caused by external agencies and that, therefore, are not due to a definite predisposition.

That we should not undervalue the influence of internal agencies on the variability appears from the following observations for which our investigations have furnished the data:

1) If the external agencies should influence the variability to any great extent, than one should expect that leaves which during their growth are subjected to a great number of continually changing agencies, should show a greater variability as they approach their full-development: but this is not so. In each of the foregoing studies it

appeared, that the variation decreases as a character reaches a higher degree of development and also therefore as it approaches the end of its development.

2) In leaves in the bud, where the influence of the environmental agencies, if not excluded at all, is certainly limited to a minimum, the greatest variability was observed.

3) In the same parts all characters are varying independently of each other; one shows e.g. an extreme plus value, whereas the other has an extreme minus or a mean value: a striking instance of this mutual independence of the characters is the following:

In *Aegopodium* the umbels with the lowest and the highest number of umbel rays were found in plants where the other umbel classes were represented in this manner:

Umbelclasses		A	B		C	D
plant 1	Number of rays	5	16	17	18	17
plant 2		20	19	31	22	—

How would it ever be possible to ascribe the fact that two umbels that grow together on the same plant and are exposed to the same external agencies should show such a quite different number of rays, to the influence of external agencies?

It is noteworthy too that one umbel may show an extremely low or an extremely high number of rays whereas an other one on the same plant show an average value.

4) In *Batrachium fluitans* the values for the length of the petiole form a kathodic series, whereas the values for the length of the blade form an anodic one. It can hardly be doubted that the petiole and the blade have been exposed to the same external circumstances.

5) In a palmate leaf each nerve varies in its own manner, and the stronger the further it is removed from nerve 1. Here too the environment is the same for the whole leaf:

6) The number of umbel rays in *Aegopodium* does not change during the development of the umbel: it is already fixed in the bud. That external agencies would influence the meristem of these buds to any extent, is hardly to be expected.

The foregoing facts, the number of which could easely be multiplied, demonstrate the great influence of internal agencies on the variability. The fact that we know little or nothing with regard to the character of these internal agencies, may not be a reason to minimize or to neglect their importance.

Because we did not intend to study the different influence of these two kinds of factors, it did not seem necessary to express a view on their mutual relation. But because of the results of our own studies we are inclined to attribute the principal part to the internal agencies, at least in so far as the development of the ideal value of a character is concerned.

GENERAL CONCLUSIONS

The study of a great number of characters in different plant species lead to the following conclusions:

1) for each character the variability is primarily determined by the position the part, by which it is exhibited, occupies in the organism:

2) when the averages calculated for the various groups of parts that occupy corresponding positions in the organism are plotted in the form of a curve, the highest value is found sometimes at the base (kathodic series) and sometimes at the top (anodic series).

3) The width of variability decreases as, for each character
   a) the part by which the character is exhibited approaches the end of its development.
   b) the group average approaches its optimum value.

The lowest degree of variability is found in characters as they exhibit their ideal development. The latter is a constant value and should be regarded as expressing a specific predisposition.

4) when the ideal value is approached, the number of variates in the central class was sometimes in the material studied by us, found to exceed that which would have been present when the curve had been a binomial one.

VI. SUMMARY

The aim of this study was to find, among groups of parts showing a variable character, one in which the variability is so strongly reduced that the character approaches constancy. This value, which we called the ideal one, is regarded as characteristic for the species.

During this investigation it appeared that this ideal value can only be found, if attention is paid to the position the parts occupy in the plan on which the plant is built (I). First of all we have tried to find in our own material a definite regularity in the variability exhibited by the various characters we studied in different plants (II). After that this regularity was tested on data obtained from other investigators (III).

In a number of leaves of *Acer palmatum* var. *septemlobum* the ratio between the length of the lateral main nerves and that of main nerve 1 (the longest nerve which at the same time is the middle one) was studied.

By comparing the averages of the varying values found for this ratio in groups of leaves occupying a corresponding position on the shoot but differing in size, we found that these averages show a slight increase when we proceed from the smaller to the larger leaves.

When we compare the averages found in groups consisting exclusively of leaves of the larger size but occupying different positions on the shoot, we saw that the averages show a continuous decrease when we begin with the leaves inserted at the base, and proceed towards those at the top of the shoot.

The averages of the varying values found for the ratio between the length of the lateral main nerves and the central one, proved to reach their highest value in the leaves at the base of the shoot, no matter which of the lateral nerves was chosen.

Besides one sees that the variation width decreases:

1) in leaves which occupy the same position on the shoot, when we proceed from the smaller to the larger ones,

2) in the groups of larger leaves when we proceed from the base of the shoot to the top.

As the ratio between the length of the lateral main nerves and that of the central one reaches its highest value in the largest and best developed leaves, we may regard a higher value of this ratio as a criterium for a better development. Whereas an increase in the value of this ratio is always accompanied by a decrease in the variation width, a decrease in the latter too may be interpreted as indicating a higher development; the optimal degree of development, its ideal value, therefore, is recognizable by the decrease of the variation width to its lowest value. When we compare the averages found for the larger leaves inserted at the base of the shoots, which are more or less well-developed (the degree of development is measured by the number of leaf pairs) we see that they are nearly the same; the variation width is in each of these groups smaller than in the shoots with a smaller number of leaf pairs. The smallest value for the variation width was found in shoots with 3 leaf pairs and for this reason we will consider the average calculated for the leaves at the base of these shoots as the ideal value of this character, i.e. the value that is characteristic for this species.

In this way the aim of this investigation, the discovery of a constant value that may be regarded as the ideal representation of a varying character, was reached (II A, a).

The same state of things was observed when we studied in the same way the ratio between the length of the lateral main nerves and the central one in *Acer cappadocicum* (II A, b) in *Platanus acerifolia* (II A, c) and in *Batrachium fluitans* (II A, d).

We found but one difference in this material, viz. that in the first named species the ideal value is, just as in *Acer palm.* v. *sept.*, found in the leaves inserted at the base of the shoot, with a decrease of the average value in the direction of the top (a kathodic series), and that in the two last species the ideal value occurs in the leaves inserted at the top (an anodic series). When for a more accurate determination of the ideal value in each of these species the degree of development of the shoot is taken into account, an almost fully constant value is obtained; in these leaves too the variation width reaches its lowest value. In this way we obtain the ideal value which is to be considered representative for the species.

From the study of the average value of the angle between the various main nerves too it appeared, that the variation width decreases as the angle approaches the ideal value. On account of this decrease in the width of variation the ideal value of this character was determined in *Acer cappadocicum* (II B, a) and in *Platanus acerifolia* (II B, b).

In the foregoing investigations it was assumed that the difference in the relative length of the main nerves or in the size of the angle between the latter, are indicative of the degree of development of the leaf and must, therefore, undergo changes during the growth of the latter.

The first-named assumption was based on the results of a comparison between average determined for groups of smaller and for groups of larger leaves occupying a corresponding position on the shoot.

In order to test the soundness of this assumption we carried out measurements on the leaves of *Tropaeolum lobbianum.* In the first place the average values and the variation width of the proportion between the length of the main nerves and the angles between these nerves were calculated in separately gathered full-grown leaves of different size. After that similar measurements were carried out in the same leaf in successive stages of its development. The necessary material was obtained by means of contact photos. No difference of fundamental importance was found between these two series of measurements (II C).

The study of the average length of leaves of *Acer palmatum* var. *septemlobum* (II D, a) *Acer cappadocicum* (II D, b) and *Platanus acerifolia* (II D, c) has shown that the average length of leaves inserted in successive positions on the shoot show a similar decrease or increase as the average of the proportion between the length of their main nerves.

Besides this it appeared that the greatest average length is accompanied by the lowest variability, and that there is no difference in this respect between leaves at the base and leaves at the top of the tree.

From a study of the averages obtained for the relative length of petiole and blade it appeared that the leaves with the highest average value show the smallest variation width. These measurements were carried out in *Acer Platanoides*, *Acer pseudoplatanus and Batrachium fluitans* (II E.)

The relative width of leaves which was studied in *Ligustrum ovalifolium* also shows the same phenomenon, viz. that the greatest width is accompanied by the lowest variability (II F).

The number of rays in the umbels of *Aegopodium podagraria* varies according to the position of the umbels on the stem, or to be more precise, according to the sequence in which they are produced. As an increase in the average number of umbel rays is always accompanied by a decrease in the variation width, the ideal value of this character is assumed to be present in the umbel which shows the lowest variation width (II G).

The method applied in the foregoing studies carried out on material collected by ourselves has also been applied to data which other investigators have found for a number of varying characters.

In the study of the size of the meshes formed by the reticulated veins of *Vitis vulpina* (III A) it appears that the variation width reaches its lowest value in the leaves in which the meshes are largest.

In a study of the internodium length of *Fagus sylvatica* (III B) the variation width proved to be smallest in those shoots in which the internodia were longest.

In *Teucrium chamaedrys* (III C) the variation width in the proportion between the number of stomata and the number of epidermis cells proved to attain its minimum value in the leaves in which this proportion reached its highest average value.

A study of the distribution of the frequency of the variates carried out for those characters of which we have ourselves investigated the variability, showed that the mean class is always best represented, as could be expected.

In the curves representing the varying characters in the groups with the ideal value, the mean class sometimes contains a larger number of variates than there are found in material showing the binomial type of frequency distribution.

The extreme plus and minus variates, which are, of course, present in a small number only, are always more numerous than was to be expected on the assumption that the frequency distribution is of the binomial type (IV).

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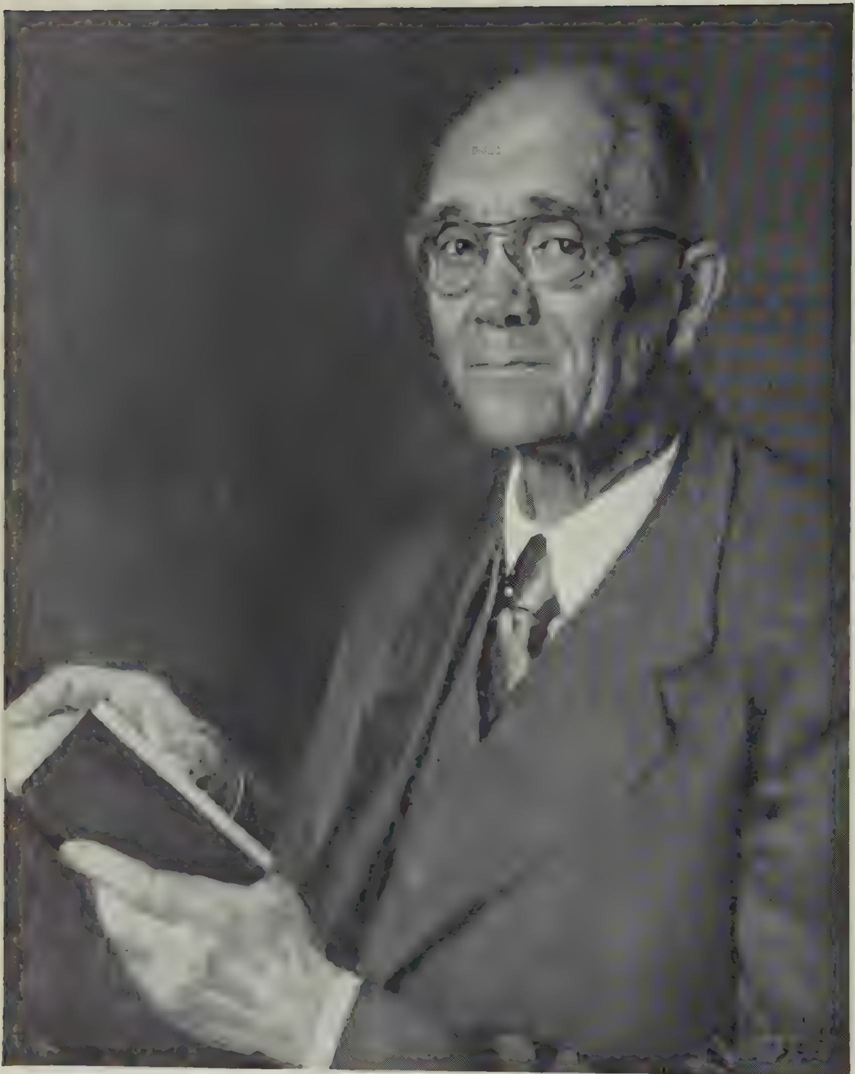

Professor Dr E. REINDERS

PREFACE

The Editorial Board of the *Acta Botanica Neerlandica* most willingly extends hospitality to the Committee in Honour of Dr E. REINDERS on his retirement as Professor of Botany, Agricultural University, Wageningen.

The contributions to this number of the KONINKLIJKE NEDERLANDSE BOTANISCHE VERENIGING's journal have been sent from diverse quarters from at home and abroad and are as many diverse tokens of esteem and regard for Reinders's activities.

The Officers also of the Koninklijke Nederlandse Botanische Vereniging wish to recognize the great merits of Reinders for Botanical Science in general and particularly his significance for Botany teaching in 'Middelbare Scholen' and Gymnasia, and Universities.

Reinders's thorough and sound knowledge of not only many subjects of botany but also of other branches of Science gave his textbooks and his publications in didactic periodicals a great influence on the development of modern Science teaching in The Netherlands. As a collaborator and the editor-in-chief of Vol. I he shares in the responsibility for Koningsberger-Reinders, Leerboek der Algemene Plantkunde, a standard work for the study of Botany in the Dutch area.

As a student of Professor Moll, Reinders concerned himself chiefly with plant morphology and plant anatomy. Appointed Professor in Wageningen in 1923 he worked at first along the principles of the Groningen-school, which soon were extended according to his own discretion. Originally a plant physiologist also Reinders encouraged plant physiological work in his laboratory, but unfortunately, being himself to much absorbed by professional duties he had no time left for research work of his own in this field.

His wide knowledge, his intellectual qualities and his broadminded views have made him a teacher the equal of whom wil not be easily found. The way in which he taught his students the fundamentals of botany has been of the utmost importance for their further agricultural studies. His students, however, above all hold in high esteem his strong personality that has been giving them more than knowledge alone. Many of his words, also those on non-botanical matters reached farther than the class room and are carried about through life. His intense and warm interest in human matters appealed to them, although a few students only will have realized all the care, time and energy bestowed on them.

The amount of work performed by Reinders cannot be estimated at its proper value. He was not easily satisfied, least of all about his own work. His judgement about persons and things always was given with complete detachment and impartiality and based on a comprehensive knowledge of the facts and thus was always well founded and appropriate.

E. VAN SLOGTEREN

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THE SECRETION OF THE SALT GLANDS OF LIMONIUM LATIFOLIUM KTZE

BY

W. H. ARISZ, I. J. CAMPHUIS, H. HEIKENS, A. J. VAN TOOREN

(Botanical Laboratory, Groningen, The Netherlands)

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INTRODUCTION

In a great number of plants living in saline habitats salt glands are found in the leaves. Among them are the Plumbaginaceae, the Frankeniaceae and some genera of the Gramineae and Tamaricaceae, as *Spartina*, *Aeluropus* and Tamarix. FABER (1923) demonstrated salt glands in Mangroves (*Avicennia marina*).

SCHTSCHERBACK (1910) studied the secretion in excised leaves of *Statice*. Structure and function of the salt glands of *Statice Gmelini* were fully investigated by RUHLAND (1915). Skelding and Winterbotham described the salt glands in the leaves of *Spartina Townsendii*.

Ruhland showed that the glands of *Statice Gmelini* consist of a complex of 16 cells rich in cytoplasm and with large nuclei (Fig. 1). The diameter of the glands is 43–46 μ. There were found on the upperside of the leaf 722 glands and on the underside 644 glands per sq. cm. Vacuoles either do not occur in the gland cells or are but of a small size.

On the outside the complex of gland cells is covered by a cutinized membrane with a cuticle, in which there are four pores (P), one in each secreting cell (A). At these places the fluid emerges. The pressure in these cells cannot extrude the cytoplasm through these pores, since a kind of membrane is present, which closes the opening in the cell wall. Between the gland cells and the adjoining cells of the tissue there is a cutinized wall which encloses the gland on all sides. Four collecting cells are bounding the gland on the side of the mesophyll. Communication between mesophyll and the cytoplasm of the outer gland cells (the cupcells) is only possible by means of these collecting cells. These cells are provided with some passage spots lying in the cutinized walls bounding the gland.

Ruhland corroborated Schtscherback's observation that leaf-segments and also isolated glands on water are capable of secretion. He arrived at the conclusion that under fairly high pressure the glands give off a fluid of which the sodiumchloride concentration is equal to or somewhat higher than the NaCl concentration in the leaf cells.

An increase of the chloride concentration in the gland he could not prove. He determined the osmotic value of the secreted salt solution by the Barger method. The difference between the osmotic concentration of the sap of the gland and the NaCl content he sometimes found to be fairly large. This must be due to the presence of organic substances.

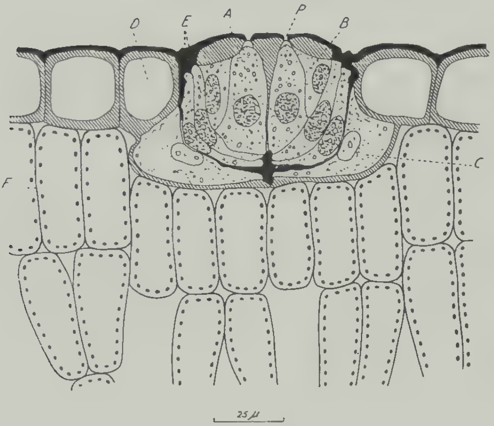

Fig. 1. Gland of *Statice Gmelini* according to Ruhland, slightly altered. A. secretion cell; P. Pore; B. adjoining cell; C. collecting cell; D. epidermal cell; E. cup cells; F. mesophyll.

After Ruhland's publication the salt glands have not been fully examined any more. They do, however, deserve attention, being organs of extraordinary efficiency in removing salt from the tissue. Ruhland found a secretion of liquid of 0.287–0.861 mg per hour per sq.cm. Our values for *Limonium latifolium* correspond with this. A 150 mg. leaflength secretes 70 mg in 24 hours.

Ruhland's fundamental experiments have been repeated and extended in my laboratory by some younger students, each working during a short period, Miss I. J. Camphuis in 1946, Miss H. Heikens in 1950 and Mr A. J. van Tooren in 1954. The results obtained have been summarized here together with some observations of my own. The plant used for these researches was *Limonium latifolium* Ktze (*Statice Limonium pseudolimonium*). In autumn potplants kept in a hot house were also used, which still showed secretion in that season.

METHOD

If a leaf or leafsegment secretes a liquid, the drops remain on the leaf and it will therefore depend on the vapour tension of the air whether evaporation of water from the drops or condensation of watervapour from the air takes place on the leaf. In order to prevent a change in concentration of the secreted fluid glass rings of 21 mm inside diameter and 3 mm height were fixed with Leicks'wax on leaf disks 3 cm in diameter, punched from the leaf. A closed chamber was obtained by fixing a glass plate on the ring with vaseline. In this way changes in concentration of the secreted drops could occur only in a very slight degree. Leafdisks 3 cm in diameter were punched from a leaf on either side of the midrib. The behaviour of disks lying on the same level was compared. The disks were put on filter paper in a dish containing water or salt solution.

After the experiment the secreted fluid in the chambers was sucked up into filter paper that had been previously dried and weighed, and the total weight was determined in a weighing bottle. The chloride content was determined after destruction of the filterpaper with HNO_3 in which $AgNO_3$ had been solved. Chloride was determined by the Volhard method.

The determination of the osmotic value of secreted fluid and sap expressed from the leaves was executed by Baldes and Johnson's osmometric method worked out in this laboratory by VAN ANDEL (1952). As comparative fluid a NaCl solution was used. The expressed sap was obtained after killing and expressing the leafdisks in a hydraulic hand press at a definite pressure. The secretion shows a great variability. By our choosing suitable leaves and gathering the results of various leaves in one experiment figures could be obtained rendering an orientation about the influence of various factors on the secreting process possible.

PRETREATMENT

Leaves of a plant from the garden contain but little chloride, about 0.23 to 0.37 %. They show no secretion. In order to obtain a proper salt secretion the intact leaves are placed beforehand with their petioles into a salt solution. Next disks 3 cm in diameter are punched from the leaves. In disks from leaves which have been for 3 hours with their petioles in 0.25 M NaCl, and which have next been placed on water, the secreted fluid amounted to 40 μg Cl in 20 hours, after a 6 hours' pretreatment 127 μg and after 22 hours 265 μg per 20 hours. The leafdisks take up the NaCl through the edges of the cut. If the latter have been greased with vaseline, no more salt is taken up.

In orientating experiments it appeared that according as the NaCl concentration is higher in the pretreatment, the chloride concentration of the secreted fluid increases. If the secretion of the leafdisks takes place on water, the increase is considerably smaller than if it takes place on a NaCl solution. In the first case no salt can be taken up during the secretion, so that owing to the loss of salt the concentration in the leaf is reduced, in the second case the salt absorption is continued, which can now be stronger, equal to or weaker than the salt secretion. This will depend on the NaCl concentration of the external solution and on the activity of the secretion process. So we found with pretreatment and secretion of the leaf on 0.08 M NaCl solution a NaCl concentration of the secreted fluid of 0.31 M; this rises on a higher concentration and amounts to 0.72 M on 0.51 M NaCl. When the secretion took place while the leaf was on water, the concentration of the secreted fluid amounted to 0.16 and 0.23 M respectively.

The use of chambers to prevent a change in concentration of the secreted fluid proved to be important. Without chambers too low concentrations of the secreted fluid were found on external solutions of low concentration, because water from the air condensed on the drops. On solutions of high concentration (over 0.42 M) too high concentrations were found without chambers, because in this case water evaporated from the drops.

TABLE I

Influence of pretreatment (24 hours) on the secretion at 25° C during 24 hours. 1951.

NaCl concentration during pretreatment	quantity secreted in mg	Cl in μg	M Cl conc. secreted fluid	M Cl conc. in leaf
Secretion on 0.47 M NaCl				
0.085 M NaCl (0.5 %)	53	931	0.49	0.17
0.171 ,, ,, (1.—)	31	381	0.34	0.18
0.342 ,, ,, (2.—)	40	656	0.46	0.28
0.513 ,, ,, (3.—)	31	596	0.54	0.39
0.684 ,, ,, (4.—)	13	171	0.35	0.16
Secretion on water				
0.085 M NaCl	48	134	0.08	0.08
0.171 ,, ,,	41	124	0:08	0.11
0.342 ,, ,,	60	299	0.14	0.14
0.513 ,, ,,	42	329	0.22	0.22
0.684 ,, ,,	37	278	0.21	0.31

Table I gives the influence of a pretreatment on various concentrations NaCl from 0.5 to 4.0 %, secretion taking place either on 2.75 % (0.47 M) NaCl or on water. A pretreatment on 2 % (0.34 M) NaCl is optimal. Both the chloride concentration of the secreted fluid and that of the leaf have been determined. When the secretion takes place on water these quantities are fairly equal. When secretion takes place on 0.47 M NaCl the concentration both in the leaf and in the secreted fluid is greatest after pretreatment on 3 % (0.51 M) NaCl. So there appears to be a distinct after effect of the amount of salt taken up during the pretreatment. In the subsequent experiments the pretreatment has been standardized as much as possible. In the experiments in 1950 pretreatment took place for 24 hours in the dark at 25° C on an external solution of 0.47 M NaCl. In 1954 pretreatment took place in artificial light at 20° or 25° on 0.34 M NaCl.

The time course of the secretion process

It has already been discussed that a leafdisk placed on water after having taken up an amount of NaCl during the pretreatment, secretes so much chloride at 25° C that the Cl concentration in the leaf is considerably reduced (Table II). This is accompanied by a fall in Cl concentration in the secreted fluid.

TABLE II

Changes in Cl concentration during secretion in leaf and secreted fluid. 1946. Pretreatment on 0.42 M NaCl. Secretion on water.

	M Cl conc. in leaf	M Cl conc. in secreted fluid
At the beginning	0.06	
24 hours pretreated.	0.25	
22 hours secretion on water	0.17	0.15
44 hours secretion on water	0.16	0.06
66 hours secretion on water	0.13	0.06

TABLE III

The time course of secretion on a salt solution and on water. 1950. Pretreatment 24 hours, dark, 25° C on 0.47 M NaCl solution.

	Secretion on 0.47 M NaCl (4 discs)			Secretion on water (6 discs)		
	quantity in mg	Cl μg	M Cl conc.	quantity in mg	Cl μg	M Cl conc.
first day	22	517	0.66	28	324	0.32
second day	25	508	0.58	31	196	0.18
third day.	22	410	0.53	32	76	0.06

Cl conc. at the beginning in leaf	0.59 M
at the end on Na Cl . .	0.39 M
at the end on water . .	0.14 M

Table III gives the course of the secretion during 3 days. During the secretion part of the leaves were placed on 0.47 mol NaCl, another part on water. When secretion took place on the salt solution, the Cl concentration of the leafdisks decreased from 0.59 to 0.39 M. The secreted fluid had a higher Cl concentration than the average Cl concentration of the leaf amounted to. The amount of secreted fluid remained fairly equal in the successive days. The Cl content of the leafdisks on water was much more reduced, from 0.59 to 0.14 M. Also in this case the amount of secreted fluid remained fairly equal on the 2nd and the 3rd day and was slightly higher than in the experiment with leafdisks on salt solution. The concentration of the secreted fluid was greatly reduced, from 0.32 to 0.06 M NaCl. It seems that at the end of this experiment a slightly higher salt concentration was present in the leaf than in the secreted fluid. If this difference is significant, it indicates that not all chloride present in the leaf can be given off by secretion. Such a regular rate of secretion during three days, which is besides nearly the same on salt solution as on water, was not found in most experiments. Usually the rate of secretion is already reduced on the second day. In Tables IV and V the secretion has been examined during 2 or 3 days for leaf disks on 0.47 M NaCl and on water. The amounts of fluid exuded on salt solution and on water are fairly equal, but both on salt solution and on water they are smaller on the second and the third day. This reduction of the secretion on the second and the third day is independent of the salt concentration of the secreted fluid, the NaCl concentration of the secreted fluids being different on salt and on water. This indicates that the amount of secreted fluid is independent of the salt concentration of the gland sap. In the course of nearly all experiments the exuded amount of fluid is reduced in successive periods. It should be borne in mind that the experiments took place in the dark. It is therefore interesting to know whether on exposure to light the strength of the secretion has a course different from that in the dark.

TABLE IV

The time course of secretion on a salt solution and on water. 1950. Pretreatment as in Table III.

	Secretion on 0,47 M NaCl (4 discs)			Secretion on water (5 discs)		
	quantity in mg	Cl μg	MCl conc.	quantity in mg	Cl μg	MCl conc.
first day	66	1444	0.62	67	652	0.27
second day	48	950	0.56	42	183	0.12

TABLE V

The time course of secretion on a salt solution and on water. 1946. Pretreatment 22 hours, dark, 0.42 M NaCl solution.

	Secretion on 0.42 M NaCl			Secretion on water		
	quantity in mg	Cl μg	M Cl conc.	quantity in mg	Cl μg	M Cl conc.
first 22 hours . . .	67	929	0.39	71	383	0.15
second 22 hours . .	38	542	0.42	37	198	0.15
third 22 hours. . .	20	336	0.47	16	29	0.05

The influence of light on the secretion appears from a comparative experiment in which after the usual pretreatment half of the leafdisks are exposed to the light, the other half put in the dark on 2 % NaCl (0.342 M). The average amount of secreted fluid in the light per disk is 50 mg with 0.544 M Cl, in the dark 16 mg with 0.520 M Cl.

TABLE VI

Influence of exposure to light on secretion. 1954. Pretreatment 24 hours, 25° C 0.342 M NaCl solution.

Secretion 24 hours 25° C on 0.342 M NaCl			
in	amount in mg	M NaCl conc.	osmometric det.
light.	97.6 (4)	0.384	0.379 M NaCl
dark.	64.1 (4)	0.393	0.413 M NaCl

In a second experiment a slightly smaller difference was found between light and dark (Table VI). During the first 24 hours 97.6 mg was secreted in the light with 0.384 M NaCl and in the dark 64.1 mg with 0.393 M NaCl. In the second 24 hours the secretion was greatly reduced both in the light and in the dark, 34.75 and 28.9 mg. In this case the osmotic value of the secreted fluid was determined with the aid of an osmometer. The concentration of the sap in the osmometer being compared with a known concentration NaCl, the osmotic values obtained have been expressed in the isotonic NaCl concentration. In the light the osmotic value was 0.379 M NaCl. In the dark 0.413 M NaCl. These values do not quite correspond with the osmotic value which may be computed from the Cl determinations. The differences, however, are too small to give an indication whether osmotically working substances other than NaCl occur in the secreted fluid.

From these experiments we may draw the conclusion that the rate of secretion is promoted by exposure to light.

INFLUENCE OF THE TEMPERATURE ON THE SECRETION

The influence of the temperature on the secretion process was investigated at 5° C and at 25° C (Table VII). Experiment A shows the secretion at 5° and at 25° C of leafdisks, one half of which secreted on water, the other half on 2.75 % (0.47 M) NaCl solution. In B and C secretion takes place at 5° C on the first day, at 25° C on the second day. From the tables it appears that when secreted on 0.47 M NaCl solution the amount of secreted fluid at 25° C is much greater than at 5° C, but that the NaCl concentration of the secreted fluid is equal at the two temperatures.

TABLE VII

Influence of temperature on secretion. Pretreatment 24 hours, dark, 25° C, on 0. 47 M NaCl solution.

A 1950 24 hours	Secretion on 0.47 M NaCl			Secretion on water		
temp.	amount in mg	Cl µg	M Cl conc.	amount in mg	Cl µg	M Cl conc.
5° C	6.6 (2)	132	0.56	13.6 (2)	268	0.56
25° C	58.0 (3)	1188	0.58	51.0 (3)	399	0.22
B 1950						
first day 5° C . .	6.4	141	0.62	10.6	220	0.60
sec. day 25° C . .	43.6	951	0.62	76.6	629	0.23
Cl content at the beginning in leaf 0.47 M						
after two days on NaCl 0.42 M						
after two days on water 0.20 M						
C 1951						
first day 5° C . .	14.0	297	0.60	22.0	320	0.41
sec. day 25° C . .	59.0	1242	0.59	78.0	527	0.19

The salt concentration in the leaf is but slightly reduced, when secretion takes place on a salt solution. If secretion takes place on water, the concentration in the leaf after the second day has got considerably reduced. At 5° C the amount of fluid secreted on water is greater than on 0.47 M NaCl solution. This must be due to the lower osmotic value of the medium and the resulting stronger turgor in the gland cells. The concentration of the secreted fluid flowing out at 25° C on water is considerably lower, because at this temperature much more sap containing NaCl is given off and as a result the Cl concentration in the leafdisk is considerably reduced, in B from 0.47 to 0.20 mol NaCl.

The temperature therefore has no influence on the concentration of the exuding sap and only regulates the amount of sap secreted.

Dependence of the secretion on oxygen

The influence of withdrawal of oxygen on the secretion was investigated in some experiments. Decrease in oxygen content of the air was obtained by binding the oxygen by means of hydrogen in a McIntosh and Fildes anaerobic jar.

The oxygen was bound to the added hydrogen gas by means of a palladium catalysator, the jar being free from oxygen after about half an hour. The withdrawal of the oxygen was checked by means of reduced aqueous methylene blue. After a 24 hours'pretreatment with 0.47 M NaCl solution the leaf disks were put in the jar for 24 hours on 0.47 M NaCl solution. Leafdisks in aerobic conditions gave 29 mg of secreted fluid with 570 μg Cl and a NaCl concentration in the secreted fluid of 0.39 M. In the absence of oxygen the secretion in 5 leafdisks averaged 1.1 mg. The secreted fluid did not contain any demonstrable Cl. Next the leafdisks were put in ordinary air, but they were no more capable of secreting.

Influence of inhibitors on the secretion

The influence of some substances inhibiting metabolism was investigated in 1950. They were KCN, Naazide, Iodoacetic acid (I.A.A.), arsenite, NaF, 2,4-dinitrophenol and phloridzine. At a low concentration KCN, I.A.A. and NaF give a distinct stimulation, arsenite a somewhat weaker one, whereas azide does not give a distinct stimulation. At a higher concentration they all give an inhibition of the secretion. Phloridzine had no influence. The results with dinitrophenol were variable (Table VIII).

TABLE VIII

Influence of inhibitors on secretion process. 1950. Pretreatment 24 hours dark 25° C on 0.47 M NaCl.

	Secretion 24 hours 25° C on 0.47 M NaCl solution	
	conc. of inhibitor giving stimulation	conc. of inhibitor giving 50 % inhibition
KCN	0.25×10^{-3} M	$7–8 \times 10^{-3}$ M
I.A.A.	5×10^{-5} M	$2\ 4 \times 10^{-3}$ M
Naazide		$2.5–7.5 \times 10^{-3}$ M
NaF	$7.5–25 \times 10^{\ 4}$ M	7.5×10^{-3} M
arsenite	10^{-7} — 10^{-6} M	$10^{-3}–5 \times 10^{-3}$ M
2,4-dinitrophenol	?	5×10^{-4} M

On determining the correlation between the amount of secreted fluid and the amount of Cl given off in a certain time with various concentrations of KCN and relating these values to the amounts of secreted fluid and Cl given off by the disks without KCN, we see that the correlation between the alterations in the two quantities under the influence of inhibitors is very great. For KCN it amounted to + 0.96 for I.A.A. + 0.91 and for Na-arsenite + 0.96. From this it follows that the concentration of the secreted fluid under influence of the inhibitors does not alter significantly. The inhibitors therefore only affect the rate of secretion.

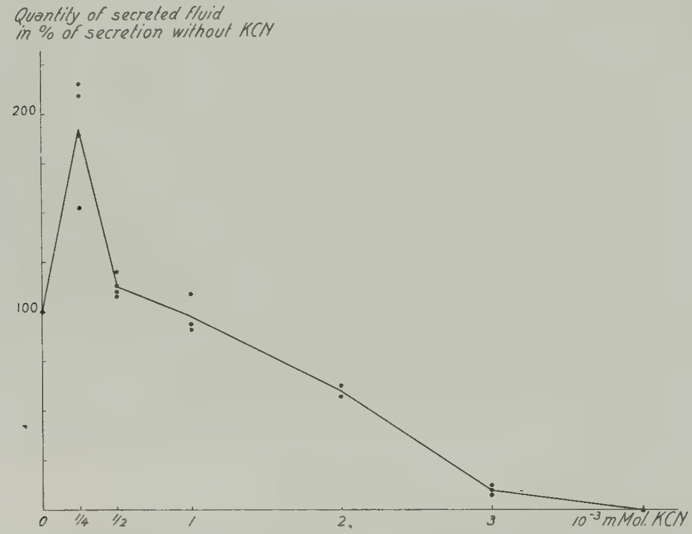

Fig. 2. Influence of KCN on the amount of liquid secreted by the salt glands of *Limonium latifolium;* the concentration remains unaltered.

The influence of KCN on the amount of secreted fluid expressed in percentage of the control without KCN is shown by Fig. 2. There is a distinct stimulation at 0.25 and 0.5 × 10^{-3} M KCN, at a higher concentration the secretion is reduced to 0. Table IX shows the influence of various KCN concentrations on the rate of secretion expressed in percentages of the control experiment without KCN.

TABLE IX

Influence of KCN on secretion. 1954. Pretreatment 24 hours, 20° C, 0.342 M NaCl, exposed to light.

Secretion 24 hours, 20° C, dark, on 0.342 M NaCl
Quantity of secreted fluid expressed in percentage of control without KCN

conc. KCN	0.00025	0.0005	0.001	0.002	0.003	0.004 M
	215 152 209 189	110 120 108 113	90 94 109	62 57	10 8 12	0 0
Average value	191	113	98	60	10	0

RELATION BETWEEN THE OSMOTIC VALUES OF THE EXTERNAL SOLUTION, OF THE EXPRESSED SAP OF THE LEAF AND OF THE SECRETED FLUID

From the data of Tables I, II, III and VII it appears that leaves that secrete on water have a chloride concentration in the secreted fluid which is equal to or lower than that of the leaf. Leaves that secrete on a salt solution have a higher chloride concentration in the secreted fluid than in the leaf. Table X shows the same phenomenon. The chloride concentration of the leaf being a quantity computed from the fresh weight of the leaf and the chloride analytically demonstrable does not imply that in the cytoplasm of the leaf cells this chloride concentration really exists. To get an impression about this, it would be necessary to know whether the chloride concentration in cell wall, cytoplasm and vacuole was equally high. A comparison of the Cl concentration in the leaf and in the secreted fluid therefore has only a limited value and no conclusion should be drawn from it concerning a possible salt accumulation in the glands.

TABLE X

Relation between the concentration of NaCl in leaf and in secreted fluid. 1946. Pretreatment 24 hours, dark, 0.42 M NaCl.

	Secretion on 0.42 M NaCl		Secretion on water	
M Cl conc.	in leaf	in secreted fluid	in leaf	in secreted fluid
at the beginning	0.06		0.06	
after the pretreatment . .	0.25		0.25	
after 22 hours.	0.30	0.39	0.17	0.15
after 44 hours.	0.28	0.45	0.16	0.06
after 66 hours.	0.23	0.33	0.13	0.06

An osmometric determination of the secreted fluid can be made with a good result with the aid of the osmometer (VAN ANDEL, 1952). In table VI it has already been found that the osmotic value found for the secreted fluid (secretion on 0.34 M NaCl solution at 25° C) expressed as an isotonic NaCl solution, corresponds with the NaCl concentration of the secreted fluid analytically determined. Both in the dark and in the light this value lies considerably higher than the osmotic value of the external solution.

It was thought desirable to compare the osmotic value of the secreted fluid also with that of the expressed leaf sap (Table XI). For the osmotic value of the sap of the leaf rather divergent values were found, but the osmotic value of the secreted fluid was always higher than that of the leaf sap. In this case too there was a great correspondence between the osmometrically determined value of the secreted fluid and the analytically found one. The differences lie within the limits of error.

These determinations had been made with leaves lying on a 2 % NaCl solution (0.342 M). In this experiment the NaCl concentration of the secreted fluid was higher than the NaCl concentration of the medium. The average osmotic concentration of the leaf sap corresponds with that of the external solution. In some experiments the osmotic concentration is higher, in the others lower than that of the external solution. This will depend on the amount of other substances than NaCl present in the sap.

TABLE XI

Osmotic conc. of leaf sap and secreted fluid. 1954.

Secretion 24 hours, 25° C, on a 0.342 M NaCl solution.

Leaf sap osmometric determination	secreted fluid osmometric determination	secreted fluid NaCl conc.
0.406 M NaCl	0.463 M NaCl	0.451 M
0.411	0.461	0.454
0.346	0.402	0.408
0.275	0.425	0.414
0.305		0.409
0.292		0.415
0.319		0.394
0.348		0.411
Av. 0.338		0.420

The osmotic value of the secreted fluid being higher than that of the leaf sap while this is about equal to that of the external solution, it is evident that the glands are capable of doing osmotic work.

TABLE XII

Influence on the secretion of increasing the osmotic value of the outer solution by adding sugar. 1954.

Pretreatment 24 hours, 25° C, 0.342 M NaCl, exposed to light.

Secretion 2 periods of 24 hours, 25° C, dark

First period. secretion	quantity in mg	Cl μg	conc. secreted fluid
0.342 M NaCl	37.2	771	0.58 M
,, ,, ,, + 0.071 M sucrose	24.8	593	0.67
,, ,, ,, + 0.142 ,, ,,	21.8	655	0.85
Second period.			
0.342 M NaCl	22.2	457	0.58
,, ,, ,, + 0.071 M sucrose	16.9	380	0.63
,, ,, ,, + 0.142 ,, ,,	11.9	398	0.97

To investigate the influence of the concentration of the external solution on the secretion process sucrose of various concentrations has been added to the outer solution (Table XII). Under the influence of the sucrose added the amount of secreted fluid is reduced and its concentration increases. So the influence of the sucrose addition is clearly shown. It may be due to the osmotic increase of the external solution or to the supply of sugar as a source of energy or to both influences. In Table XIII the influence of the increase of osmotic value of the outer solution through addition of higher sugar concentrations on the NaCl concentration of leaf and secreted fluid has been traced.

As already discussed above the NaCl concentration in the secreted fluid is considerably higher than in the leaf in such cases. Addition of sugar gives a lower rate of secretion. The NaCl concentration in the leaf remains about the same, that in the secreted fluid is considerably increased with the greatest addition of sugar.

TABLE XIII

Influence of increasing the osmotic value of the outer solution on the NaCl conc. in leaf and in secreted fluid. 1954.

Pretreatment 24 hours, 25° C, 0.342 M NaCl, exposed to light.

	Secretion 24 hours, 25° C, dark		
	quantity in mg	M Cl conc. in secreted fluid	M Cl conc. in leaf
Secretion on 0.342 M NaCl	31.9	0.418	0.336
,, ,, ,, ,, ,, + 0.150 M sucrose	15.4	0.378	0.318
,, ,, ,, ,, ,, + 0.250 ,, ,,	11.8	0.501	0.324

TABLE XIV

Influence on the secretion of increasing the osmotic value of the outer solution by adding sugar. 1954.

Pretreatment 28 hours, 25° C, 0.342 M NaCl, exposed to light.

	Secretion 24 hours, 25° C, dark		
	quantity in mg	M Cl conc.	osmotic value osmometrically determined
Secretion on 0.342 M NaCl	38.2	0.358	0.412
,, ,, ,, ,, ,, + 0.086 M sucrose	37.0	0.558	0.613
,, ,, ,, ,, ,, ,, + 0.172 ,,	17.6	0.688	0.750

Table XIV shows the influence of an increase in osmotic value of the external solution through addition of sugar on the osmotic value of the secreted fluid. In this experiment both an analytical determination of the NaCl concentration of the secreted fluid and an osmometric determination of the NaCl concentration which is isotonic with the secreted fluid was made. It appears that in every case the osmometrically determined value lies higher than the NaCl concentration of the secreted fluid, so that besides NaCl a small amount of a different substance must have been present in the secreted fluid. Through addition of sugar here too the NaCl concentration of the secreted fluid increases greatly.

In Table XV experiments are shown in which $MgSO_4$ has been added to the external solution instead of sugar, in order to investigate a substance which would act especially osmotically. NaCl has been applied in two different concentrations as well.

Here too an addition of NaCl brings about a somewhat smaller amount and a higher concentration of the secreted fluid, resulting in a higher amount of Cl given off. On enhancing the concentration with $MgSO_4$ a considerably smaller amount of secreted fluid is obtained, while the Cl concentration of the secreted fluid increases less. The result is a smaller total amount of Cl being given off than without the addition of $MgSO_4$. In principle the influence of sugar, NaCl and $MgSO_4$ corresponds, so that the action of these substances is based in the first place on their osmotic influence.

TABLE XV

Influence on the secretion of increasing the osmotic value with magnesium sulfate. 1954.

Pretreatment 28 hours, 20° C, 0.342 M NaCl, exposed to light.

	Secretion 28 hours, 20° C, dark		
	quantity in mg	Cl μg	M conc. NaCl in secreted fluid
secretion on 0.171 M NaCl	50.3	516	0.288
,, ,, ,, ,, ,, + 0.081 M $MgSO_4$	25.0	326	0.366
,, ,, 0.342 M NaCl	42.4	647	0.429

MECHANISM OF THE GLAND SECRETION

The action of the gland cells is considered by Ruhland as an active process secreting water in which salts and organic substances are present in a varying quantity. If the gland cell is rich in salt, the secreted fluid is rich in salt as well, if the gland cell is poor in salt, if for instance the secretion takes place on water, the secreted fluid is also poor in salt. In his opinion the glands work without selectivity. They are no filtration hydathodes, but they squeeze out water actively. Osmotic work is not turned out by the gland cells according to Ruhland.

Our data are not yet adequate to give a full explanation of the secreting process. They supplement Ruhland's results and differ from them mainly in one respect, as we found that the osmotic value of the secreted sap can be higher than that of the expressed sap of the leaf, i.e. that the glands can perform osmotic work. It was proved that secretion is an active process dependent on the presence of oxygen and demonstrated that temperature, light and inhibitors influence secretion. They change the rate, but leave the NaCl concentration unaltered. This proves that the secretion process depends on cell metabolism.

In a leaf on a salt solution the NaCl concentration of the secreted fluid is higher than the NaCl concentration of the leaf. It being unknown, whether the chloride present in the leaf is found in wall, cytoplasm or vacuole, nothing can be stated about the actual NaCl concentration in the cytoplasm of the leaf cells and it is therefore unknown whether the NaCl concentration in the secreted fluid is actually higher than in the cytoplasm of the leaf cells.

The osmotic value of the expressed sap of the leaf seems to correspond more or less with that of the external solution (Table XI). The osmotic value of the secreted fluid, however, can be considerably higher, about 0.1 M sugar, than that of the expressed sap of the leaf. This proves that osmotic work must be done to keep the secretion going.

The apertures in the cutinized outer wall of the secretion cells enable fluid to leave the cytoplasm. It is assumed that sap will be given off from the secretion cells under the influence of the turgor pressure of these cells. The cytoplasmic fluid is not likely to flow out quite unchanged. Great molecular substances will naturally remain in the cytoplasm. NaCl is secreted in any case and in some cases organic substances are likely to be secreted as well. Ruhland states that 25 to 40 % of the dry matter of the secreted fluid of *Statice gmelini* may be attributable to organic substance. With leaves on destilled water he obtained secretion for 34 days. The secreted amount of fluid was then reduced to one fourth, the concentration of the dry substance being reduced to less than one third. If the water in his experiments has been changed, we may assume that after a day or two the leaves did not give off any more NaCl. The secretion, however, continued, though the rate decreased, the concentration being reduced as well. This would indicate a secretion of organic substances. The results of table XIV show that also in the case of *Limonium latifolium* a small quantity of other substances than NaCl may be found in the secreted fluid. We did not find, however, any secretion of fresh leaves of *Limonium latifolium* unless NaCl was administered. As far as we know there is no exudation of pure water. The subject deserves to be further examined especially in *Statice gmelini.*

Though the osmotic concentration of the sap in the gland cells cannot be directly determined, it can be estimated since the osmotic concentration of the secreted fluid must be equal to or somewhat smaller than the osmotic concentration of the sap of the gland cells. This will depend on the permeability of the plasm in the pores. The difference is caused by not exuded substances and will be relatively small when salt is present in high concentration.

The osmotic concentration of the sap equals the suction pressure plus the turgorpressure in the gland cells. In order to produce a sufficient turgorpressure the osmotic value of the gland sap has to be considerably higher than that of the external solution. The turgor can be reduced by enhancing the osmotic value of the external solution. A restoration of the turgorpressure needs an uptake of osmotically active substances in the gland cells till their suction pressure has become higher than that of the external solution.

It appears from Table XIV that the quantity of sap exuded is reduced by enhancement of the osmotic concentration of the external solution and that secretion is continued after a considerable increase of the osmotic concentration of the sap in the gland cells, which results in a higher NaCl content and a higher osmotic value of the secreted liquid. These experiments are in accordance with the assumption that the secretion is dependent on the turgorpressure of the gland cells. We have already discussed that the amount of secreted fluid is independent of the salt concentration of the gland sap (cf. p. 326). Seeing the NaCl concentration in the gland cell may vary, it is evident that the sap expressed under the influence of the turgorpressure may also be richer or poorer in NaCl.

Ruhland had already shown that secretion can take place against a fairly high pressure from outside, so that a coat of wax put on the surface of the leaf is pressed upwards. From a comparison of the anatomical structure of the glands of *Limonium* with those of *Spartina Townsendii* Arisz (1955) has drawn the conclusion that the fluid is squeezed out by the pressure in the gland cell. In *Spartina* the aperture through which the sap exudes lies in the wall of an adjoining epidermal cell. Here the pressure in the gland cell must be transferred through the symplasm to the epidermal cells.

All these data indicate that not the exudation of the liquid from the cytoplasm is the energy requiring process in the secretion but keeping up the pressure in the gland cells by introducing substances into these cells.

The problem therefore is how this pressure and the salt concentration in the gland cells is being maintained and regulated. An active mechanism must carry a solution of water with salts and organic substances into the gland cells. A mechanism that carries water and dissolved substances simultaneously is unknown. It should, therefore be considered whether the introduction of salt and organic substance or that of water is the energy requiring process.

Processes of active salt uptake are well known. If by an active uptake of substance the pressure in the gland cells is maintained, the production of sap by the gland cells will take place at a constant rate. In leaves placed on water, the NaCl concentration of the secreted sap is reduced, the amount of sap being as great as in leaves on a salt solution, which have a much higher NaCl concentration of the secreted sap. This must be due to the fact that in both cases the pressure in the gland cells regulating the amount of fluid secreted, is equally great.

Whereas in leaves rich in NaCl especially NaCl will be pumped into the gland cells to keep the pressure up, in leaves on water the pressure is likely to be maintained by introduction of partly other substances than NaCl especially when these other substances get lost in the secreted fluid.

Temperature, light and inhibitors affect this active process that regulates the pressure in the gland cells and together with it the strength of outflow.

Some investigators have assumed an active water uptake into the cell. An efficient water uptake into the cell requires a membrane that can only be passed with the aid of an energy requiring process. If for the glandular action we assume as only active process an active water uptake into the gland cells, it is hard to understand how owing to temperature, light and inhibitors more fluid can be secreted without the concentration of the secreted fluid being reduced. This requires a simultaneous active salt uptake, organized in such a way that it is equally influenced by the factors mentioned as the active water uptake. The active salt uptake, however, would make the active water uptake superfluous.

Until we have more data at our disposal, it seems to us that the above conception of the mechanism as a system that carries salts into the gland cells actively and by doing so causes a pressure in them resulting in an expression of sap from the pores, is the most acceptable. A definite opinion on the secretion mechanism can only be given, when the biochemical processes on which it is based, are known.

Here we may refer to the correspondence of this process with the secretion of a salt solution to the vessels with the bleeding of the root, discussed by Arisz (1955).

Summary

The concentration of NaCl in the external solution during the pretreatment influences the secretion by the salt glands. A pretreatment with 2 % to 3 % is most favourable, then both the amount and the concentration of the secreted fluid and also the NaCl concentration in the leaf are greatest (Table I).

The rate of secretion is constant during the first few days or is reduced (Tables III, IV, V). The amount of secreted fluid is usually somewhat higher on water than on salt owing to the lower osmotic value of the external solution.

The NaCl concentration of the secreted fluid may either increase or decrease during the secretion on a salt solution. With secretion on water there is always a decrease.

When exposed to light the amount of secreted fluid increases. The concentration of the secreted fluid does not change (Table VI).

If temperature is raised from 5 to 25° C the rate of the secretion of fluid increases 7 times. The concentration of the secreted fluid remains fairly equal, unless the secretion takes place on water (Table VII). Oxygen is required for the secretion.

In a low concentration inhibitors increase the rate of the secretion of fluid, in a high concentration they inhibit it. The NaCl concentration of the secreted fluid remains unchanged (Tables VIII and IX, Fig. 2).

The osmotic value of expressed leaf sap varies. The average osmotic value is equal to the osmotic value of the medium (Table XI). The osmotic value of the sap secreted by the gland is higher than the osmotic value of the expressed leaf sap (Table XI). For the secretion osmotic work is done.

The osmotic value of the secreted fluid, computed as NaCl solution, corresponds with the NaCl concentration of the secreted fluid (Table VI). In an other experiment (Table XIV) with secretion on sugar plus salt solution it was greater than the NaCl concentration of the secreted fluid. This indicates the presence of other substances in the secreted fluid. Increase of the osmotic value of the external solution:

(A) by *sugar* (Tables XII, XIII, XIV) decreases the amount of secreted fluid and increases the NaCl concentration and the osmotic value of the secreted fluid.

(B) by NaCl (Table XV) alters the amount of secreted fluid but little. On addition of too much diluted salt solutions or water there is a decrease of the amount of secreted fluid. The NaCl concentration in the secreted fluid increases. The total loss of Cl has increased.

(C) by $MgSO_4$ (Table XV) gives a reduction of the amount of secreted fluid and an increase of the NaCl concentration of the secreted fluid. The total loss of Cl has decreased.

The mechanism of the secretion may be considered as a system that introduces salts actively into the gland cells and by doing so causes a pressure that results in a squeezing of sap through the pores out of the gland cells. The amount of expressed sap depends on the pressure in the gland cells. The latter may be osmotically influenced by the external solution.

The composition of the expressed sap depends on the substances accumulated in the gland cells and on the permeability at the pores.

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